STUDIES ON THE MORPHOLOGY, FEEDING BEHAVIOUR AND BREEDING BIOLOGY OF SKUAS (FAMILY STERCORARIIDAE) WITH REFERENCE TO KLEPTOPARASITISM

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CANDIDATE'S DECLARATION

I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is of my own composition. No part of this work has been submitted for any other degree.

Richard W.G. Caldow

ABSTRACT

1) The kleptoparasitic success rates of light and melanic Arctic skuas did not differ significantly. Great skuas were significantly more successful than Arctic skuas in inducing their victims to release their fish, and in securing these dropped fish.

2) Both species of skua had significantly higher kleptoparasitic success rates than "gulls" chasing the same range of species at the same location.

3) Groups of Arctic skuas were significantly more successful in inducing their victims to release their fish than were solitary Arctic skuas. This was not the case for great skuas. Kleptoparasitic association between skuas seems to be an example of a selfish group.

4) Chases by great skuas were more likely to be successful if the victim was high above the water when the chase began and was slow to react to the attacking skua. Chases by Arctic skuas were more likely to be successful if the skua approached to within 1 metre of the victim and if the chase was towards the cliff.

5) Arctic skuas and great skuas differed in the locations at which they concentrated their kleptoparasitic efforts and in the methods of attack which they employed. Generally, Arctic skuas relied less on rapid descending stoops from above their victims than did great skuas and used flapping flight in a significantly higher proportion of chases than great skuas.

6) Arctic skuas rearing chicks had rates of energy expenditure equivalent to 3.3 - 3.9 times BMR. The rate of energy expenditure by breeding great skuas which were rearing chicks was equivalent to 5.0 - 5.8 times BMR. Energy expenditure was greater than in the mid-1970s when host availability was higher.

7) The daily energetic reward from kleptoparasitism was sufficient to meet the daily energy requirements of three pairs of great skuas and two pairs of Arctic skuas with normal brood sizes. A pair of Arctic skuas with three chicks had a negative energy balance.

8) Mean clutch size, egg volume and hatching success of Arctic skuas in 1987 were as high as in 1979. Mean clutch size and hatching success of great skuas were as high in 1987 as in the mid-1970s.

9) The growth rates of skua chicks in 1987 were not as high as in the mid-1970s. The fledging success of great skuas in 1987 was lower than in the mid-1970s. The breeding success of Arctic skuas was significantly lower in 1987 than in 1979 due to extremely heavy predation of Arctic skua fledglings by great skuas in 1987.

10) Breeding skuas spent considerably more time foraging during the latter part of the pre-fledging period in 1986 and 1987 than in the mid-to-late 1970s. In 1986 and 1987, great skuas frequently left their chicks unguarded and hence open to predation by neighbouring skuas.

11) Arctic skuas and great skuas were found to differ significantly in many aspects of their morphology from equivalently-sized gulls. On theoretical grounds these differences appear to enhance the kleptoparasitic flight performance of skuas relative to that of gulls.

12) It is suggested that these morphological differences between gulls and skuas, although beneficial to skuas' kleptoparasitic flight performance, are not the result of specialisations which evolved specifically for this purpose. It is proposed that skuas are morphologically pre-adapted to behaving kleptoparasitically as a consequence of their evolution to a more predatory way of life than gulls.

13) It is suggested that the highly kleptoparasitic nature of skuas is the result of morphologically and behaviourally pre-adapted species utilising this feeding technique when possible and profitable to do so.

14) The flight muscles of a great skua and a herring gull were not found to contain any "white" fibres. The pectoralis major and pectoralis minor muscles of the great skua had higher levels of oxidative and glycolytic enzyme activity than the equivalent muscles of the herring gull.

15) The possession of morphological adaptations which enhance the kleptoparasitic success rate of skuas could be of benefit in three ways. Firstly, with a higher success rate this feeding technique may be profitable enough to allow skuas to switch from other feeding techniques, in the face of a food shortage, and to continue to breed successfully when a lower success rate would preclude this possibility. Secondly, a higher success rate reduces the time and energy expenditure required to collect a given amount of food. Under conditions of food shortage, this could be of great importance in maintaining adult energy expenditure below some critical level above which parental survival may be jeopardised, and in minimising the likelihood that parents will have to leave their chicks unattended. Thirdly, the ability to feed successfully by kleptoparasitism may allow skuas to breed in areas of the world where, with a lower success rate, they could not.

CONTENTS

Chapter 1

Introduction.

It is generally held that the skuas (Family Stercorariidae), gulls and terns (Family Laridae), and the noddies and skimmers (Family Rynchopidae) (after Hoffman (1984)), are more closely related to one another than to any of the other members of the Order Charadriiformes to which they belong (Strauch 1978, Michevich and Parenti 1980). However, the relationships between these various families of birds and between the individual species within these families have been, and still are, the subject of much debate (Dwight 1925, Peters 1934, Moynihan 1959, Hudson et al.1969, Schnell 1970a,b, Strauch 1978, Michevich and Parenti 1980, Hoffman 1984). Hoffman (1984), in a study of the phylogeny, feeding behaviour and wing-structure of the superfamily Laroidea suggested that the evolution of the skuas, gulls, terns, noddies and skimmers, as a group, came about as the result of an "extensive radiation, apparently in response to aerial feeding opportunities". Hoffman (1984) presented four scenarios of the evolutionary history of the present-day Laroidea and concluded that their most likely common ancestor was a proto-gull or proto-tern. He also concluded that the evolution of the Stercorariidae, from whichever ancestor, was the result of increasing specialisation to feeding by predation and kleptoparasitism.

The term kleptoparasitism was first coined by Rothschild and Clay (1952) in reference to the theft of a food item from an individual of one species by an individual of another species. Among birds

kleptoparasitism or piracy has become almost synonymous with skuas and frigatebirds (Order Pelecaniformes Family Fregatidae), but these are by no means the only birds to exhibit this feeding behaviour. In a review of the literature Brockman and Barnard (1979), found that this feeding behaviour had been recorded in over 100 species of bird belonging to 12 orders. Brockman and Barnard (1979) pointed out that certain orders of birds (Falconiformes, Charadriiformes, Pelecaniformes and Ciconiiformes) contain a disproportionately large number of kleptoparasitic species. The only families of birds in which more than 25% of the species are known to indulge in kleptoparasitism to some extent are the Fregatidae (frigatebirds), Stercorariidae (skuas), Laridae (gulls and terns) and Chioninidae (sheathbills) (Brockman and Barnard 1979).

The highly conspicuous nature of kleptoparasitic interactions, which may have resulted in over-estimation of the importance of this style of feeding to kleptoparasitic species such as skuas and frigatebirds, makes this feeding technique much more amenable to investigation than other methods of feeding employed by seabirds. Consequently kleptoparasitic feeding by seabirds has been extensively studied (Hatch 1970, 1975, Grant 1971, Hopkins and Wiley 1972, Dunn 1973, Andersson 1976, Hulsman 1976, Nelson 1976, Fuchs 1977, Kallander 1977, Verbeek 1977, Arnason 1978, Arnason and Grant 1978, Furness 1978a, 1981a, Taylor 1979, Furness and Furness 1980, Burger 1981, Burger and Gochfeld 1981, Forssgren 1981, Maxson and Bernstein 1982, Greig et al.

1983, Hudson 1985, Thompson 1986, Birt and Cairns 1987, Rice 1987).

The attack strategies employed by kleptoparasites differ within and between species, and depend on the species of host which is attacked and the location. One of the most peculiar techniques is that of lesser sheathbills (Chionis minor) which throw themselves against rockhopper penguins (Eudyptes chrysocome) which are in the process of feeding their chicks, and steal the food spilt as a result of the collisions (Burger 1981). Similar tactics are sometimes employed by herring gulls (Larus argentatus) kleptoparasitising shags (Phalacrocorax aristotelis) (pers.obs.). Gulls and terns frequently attack victims which are on the ground by walking or flying towards them rather than pursuing them in flight (Hulsman 1976, Burger and Gochfeld 1981, Greig et al. 1983, Hudson 1985, Thompson 1986, Rice 1987). However, the most typical form of attack is the high speed aerial pursuit which is exhibited by gulls and terns (Hatch 1970, 1975, Hopkins and Wiley 1972, Hulsman 1976, Burger and Gochfeld 1981, Thompson 1986), skuas (Grant 1971, Andersson 1976, Arnason 1978, Arnason and Grant 1978, Furness 1978a, 1981a, Taylor 1979, Furness and Furness 1980, Maxson and Bernstein 1982, Birt and Cairns 1987) and frigatebirds (Nelson 1976).

In many respects it is reasonable to consider skuas in the marine ecosystem as analogous to raptors in terrestrial ecosystems since each are the top avian predators of their respective food chains or webs. The similarities between skuas and raptors (particularly those which are avian predators) are numerous and embrace morphological

characteristics; such as overall plumage colouration, various features of the bill, feet and legs (Furness 1987a) and the possession of reversed sexual size dimorphism (Andersson and Norberg 1981, Furness 1987a), as well as behavioural traits such as role differentiation between the sexes during the breeding season. Although the proximate aim of kleptoparasitic chases by skuas (to steal food) differs from that of attacks by raptors (to catch and kill the victim), the ultimate purposes are the same: to obtain food. However, whereas it is relatively difficult to study the feeding behaviour of avian predators (Newton 1986), kleptoparasitism is, by its very nature conspicuous, and occurs in open spaces at predictable locations and times of year. Thus kleptoparasitism affords the possibility of studying various facets of avian interspecific aerial interactions which are otherwise difficult to investigate, for example; the success rates of attacks, factors which affect the success of attacks, success in attacking different species of victim, the different methods of attack employed by different species of attacker in relation to their flight capabilities and the benefits of forming group attacks. Thus the kleptoparasitic feeding behaviour of great skuas (Catharacta skua) and Arctic skuas (Stercorarius parasiticus) which were breeding on the island of Foula, Shetland, was studied with a view to investigating these topics (chapter 2). The study of skuas' kleptoparasitic feeding habits was used to address two theoretical problems which are outlined below.

Brockman and Barnard (1979) suggested that kleptoparasites could be divided into "specialists", such as skuas and frigatebirds, and "opportunists" such as gulls and terns. One of the main arguments against this idea rests on the counter-intuitive finding that, on the whole, "specialists" are no more successful in stealing food from their hosts than are "opportunists" (Furness 1987b). However, the results of Arnason and Grant (1978) and Forssgren (1981) indicate that when "specialists" and "opportunists" are compared under identical conditions, the former are more successful. This important issue was investigated by comparison of the kleptoparasitic success rates achieved by gulls and skuas chasing the same host species at the same location (chapter 2).

The hypothesis that the adaptiveness of external polymorphism can be explained by apostatic selection through density-dependent predation was first suggested by Clarke (1962a,b). Payne (1967) and Paulson (1973) inverted this argument and suggested that polymorphisms in predatory species could be maintained by apostatic selection due to the use of search images by intelligent prey with reasonable visual acuity. The hypothesis, as stated by Paulson (1973) is as follows, "The rarer of two morphs of a predator should be less familiar to a potential prey individual and thus have a greater chance for successful capture of that individual. This slight advantage of the rarer morph should lead to balanced polymorphism in the population".

The role of apostatic selection in maintaining the marked plumage polymorphism of Arctic skuas has been the subject of a great deal of

research and debate (Paulson 1973, Arnason 1978, Furness and Furness 1980, O'Donald 1983, Rohwer 1983, Furness 1987a). In view of the apparently contrary results of Arnason (1978) and Furness and Furness (1980) (although see Rohwer 1983), it was decided that this point merited further investigation (chapter 2). Rohwer (1983) suggested that experimental manipulation of the two phases of Arctic skuas in a population by means of selective removals could be used to test the validity of the apostatic selection hypothesis. No such removals were actually carried out in this study since natural processes over the recent past have produced just such changes in the relative frequencies of the two phases of the Arctic skua on Foula. Since detailed studies of kleptoparasitism by skuas have been carried out on Foula in the past (Furness 1978a,1980,1981a), it was possible to study changes in the success rates of the two phases of Arctic skua over a period of time during which their relative frequencies in the population have changed, and hence to investigate the validity of the apostatic selection hypothesis (chapter 2).

The results of these previous studies also allowed an investigation of changes in the success rates of great skuas and changes in the host selection patterns of both species of skua, in relation to changes in host availability (chapter 2).

Kleptoparasites usually have a variety of alternative methods of feeding available to them (Furness 1977, Kallander 1977, Verbeek 1977, Kushlan 1978, Brockman and Barnard 1979, Burger 1981, Greig et al.

1983). However, few studies have investigated the profitability of kleptoparasitism in relation to that associated with other feeding techniques. Kushlan (1978) showed that the cost-benefit ratio of great egrets (Casmerodius albus) was higher when feeding kleptoparasitically than when using the more typical stand-and-wait feeding technique. He concluded that the use of this feeding technique by the egrets represented non-rigorous foraging and hence that "energy return need not always be optimised over the short term". However, since " natural selection ultimately operates only by differential reproductive success" (Pianka 1976), selection against kleptoparasitic feeding behaviour should only occur if it is not as successful in terms of long term reproductive success as the other feeding strategies employed by the species (Brockman and Barnard 1979).

Furness (1980) pointed out that the use of kleptoparasitism by Arctic skuas in Shetland is not subject to this control as they have no alternative to feeding in this way when breeding there. Nonetheless, for Arctic skuas to breed successfully in Shetland the energetic reward from kleptoparasitism should approximately equal the energy requirements of breeding birds and their chicks. This point was investigated by carrying out detailed time-budget studies of breeding Arctic skuas and comparing daily energy expenditure with net assimilated input per day which was calculated on the basis of the amount of time spent foraging and the success rate of skuas in securing fish from chases (chapter 3).

Great skuas in Shetland obtain very little of their food by kleptoparasitism (Furness and Hislop 1981). They feed mainly by catching sandeels (Ammodytes marinus) for themselves or by scavenging discarded whitefish from behind fishing boats (Furness 1979, Furness and Hislop 1981, Hudson 1986, Hudson and Furness 1988). Since great skuas do breed successfully in Shetland, kleptoparasitism, if it is a feeding strategy, must be an energetically profitable one for its use to persist in the population, particularly at the time of year when foraging optimisation is most likely to be important (Kushlan 1978). This point was investigated in the same way as for Arctic skuas (chapter 3). Since it is very unlikely that the study pairs of great skuas fed entirely by kleptoparasitism, the results of these calculations are only theoretical in this case. However,the results indicate whether great skuas could breed successfully when feeding entirely in this way. This could have important repercussions for the Shetland population of great skuas in view of the current decline in the availability of sandeels.

In order to obtain a background picture of the environmental conditions which prevailed during the two seasons in which the kleptoparasitic feeding behaviour of skuas was studied, various aspects of the breeding biology of skuas were also investigated. Since skuas in Shetland spend little time away from their territories when not foraging (Furness and Hislop 1981), the territorial attendance patterns of breeding skuas were studied to serve as an indicator of the amount of time which skuas spent foraging and by implication of

the level of food availability (chapter 4). In addition, egg sizes, clutch sizes, hatching success, fledging success and chick growth-rates of great skuas and Arctic skuas were recorded in 1987 (chapter 4).

Brockman and Barnard (1979) suggested that one of the pre-requisites for the evolution of aerial kleptoparasitism is the possession of morphological adaptations to enhance aerial agility. They suggested that "specialist" kleptoparasites such as skuas and frigatebirds are "built for sustained and manoeuvrable flight", and cited the small unwebbed feet, vestigial uropygial gland and large wingspan relative to body mass as morphological specialisations by frigatebirds. Barnard (1985) suggested that this unique morphology of frigatebirds is the result of adaptations specifically to enhance kleptoparasitic success. Brockman and Barnard (1979) presented no examples of morphological adaptations of skuas. Therefore, one of the aims of this study was to determine whether the morphology of skuas differs from that of their nearest relatives (ie gulls, although see Hoffman (1984)) in ways which would be beneficial in terms of sustained and manoeuvrable flight. Such differences would lend support to the idea that the development of "specialised" kleptoparasitic behaviour either requires, or has resulted in, the possession of particular morphological adaptations. The possibility that any such morphological differences could have evolved for reasons other than as a consequence of an asymmetric evolutionary arms race between attacker and host

(Dawkins and Krebs 1979, Furness 1987b) to enhance kleptoparasitic success, is discussed.

Predictions of the ways in which skuas should differ from gulls if they possess specialisations for high speed chases were derived from a study of the theory of bird flight of which a brief summary is presented in chapter 5. The morphological comparison between skuas and gulls involved the measurement of various external features which determine flight capabilities, for example wing loading and aspect ratio, an assessment of the flexural stiffness of flight feathers, measurements of the wing bones and an assessment of flight muscle mass and volume (chapter 6).

The proportions of different fibre types present in the major flight muscles of birds differ between species and simultaneously reflect their flight requirements and indicate the limits of their flight capabilities (George and Berger 1966, Kiessling 1977, Talesara and Goldspink 1978, Rosser and George 1986). Since aerial kleptoparasitism requires agility and high flight speeds it was predicted that the flight muscles of skuas and gulls would differ in their ultrastructure. Thus the flight muscles of skuas and gulls were compared by means of histochemical techniques (chapter 7).

The overall aim of this thesis is to present data on the kleptoparasitic behaviour of skuas during the breeding season, to consider the importance of kleptoparasitism to skuas' breeding success and to explore anatomical and physiological adaptations of skuas that may enhance their success as kleptoparasites.

Throughout this thesis the Latin name of each species is given immediately after that species is first mentioned within the text of each chapter. References to results as being either significant or not significant refer to statistical significance. Results were considered to be statistically significant if the probability of chance occurrence was less than 0.05.

Chapter 2

Kleptoparasitic feeding behaviour of skuas.

Introduction

This chapter describes the methods of collection and analysis of data concerning the kleptoparasitic feeding behaviour of skuas. The results of these analyses are discussed in relation to the extensive published literature on kleptoparasitism and various theories regarding kleptoparasites and kleptoparasitism which were mentioned in the previous chapter.

Methods

1) Recording of observations

Observations of the kleptoparasitic interactions between skuas and their victims were made from two clifftop sites on the island of Foula, Shetland. Both sites afforded unrestricted views along considerable lengths of cliff on which large numbers of puffins (Fratercula arctica), guillemots (Uria aalge) and razorbills (Alca torda) bred. Interactions observed at Kittiwakes' Haa (75m above sea-level) were almost exclusively initiated by great skuas (Catharacta skua), while those observed at Heddlicliff (40m above sea-level) were almost exclusively initiated by Arctic skuas (Stercorarius parasiticus).

Between mid-June and mid-August 1986, watches were carried out at each site on alternate days. Between the end of May and mid-August 1987, watches were carried out at each site at approximately weekly

intervals. Observation periods were divided into watches of one hour during which either kleptoparasitic interactions or the arrivals of fish-carrying auks were studied. During watches of kleptoparasitic interactions, all interactions between skuas and their victims, which occurred within a pre-determined volume of air in front of the cliff, were recorded. For each interaction observed in 1986 the following parameters were recorded whenever possible; the species of victim, the species and phase (in the case of Arctic skuas) of the attacker(s), the number of attackers, the duration of the chase, whether the victim lost its fish, how the victim lost its fish (ie dropped, stolen from its bill or lost on impact with the water), whether the fish were secured by anything, which bird secured the fish (ie the chase initiator, a joiner to the chase, or a gleaner), where the successful bird secured the fish, whether contact occurred between the victim and the attacker(s), whether the attacker(s) used flapping flight in the course of the chase, whether the attacker(s) made any rapid changes in direction during the course of the chase, whether the attacker(s) stooped down on the victim with closed wings, and whether the victim landed on or dived into the water.

Several other variables which were recorded for each interaction, were not of the clearly defined nature of those listed above. These variables, and the categories recorded are listed below;

1) Speed of reaction of the victim to the attacker(s). This was classified (following Furness 1978a) as; fast (1), if the victim took evasive action as soon as the chase initiator began its approach, slow

(3), if the victim did not take evasive action until the attacker(s) were very close to it, or intermediate (2), if the victim took evasive action after the initiator had begun its approach but was still some distance from the victim.

2) Minimum distance between the attacker(s) and the victim. This was classified as; less than one metre (1) or greater than one metre (2).

3) Initial height of the initiator relative to that of the victim. This was classified as; above (1), the same height (2), or below (3).

4) Initial position of the initiator relative to the direction of flight of the victim. This was classified as; in front (1), to the side (2), or behind (3).

5) The direction of the chase relative to the cliff. This was classified as; towards (1 yes, 0 no), parallel (1 yes 0 no), or away (1 yes 0 no).

6) The height of the victim above sea-level at the start of the chase. This was clasified as; high (1), moderate (2), or low (3). No attempt was made to record absolute heights.

7) How the attacker(s) approached the victim. This was classified as; descending flight (1), level flight (2), or ascending flight (3).

Of the parameters mentioned above, only the first nine were recorded for each interaction observed in 1987. However, one new variable; the number of fish secured, was recorded for each successful interaction.

In both 1986 and 1987, the arrival patterns of fish-carrying auks was studied by recording the numbers of each species of auk which

arrived at the cliff with fish during each hour long watch. Birds were counted only if they landed between the point of observation and the landmark on the cliff which defined the furthermost limit of the airspace within which chases by skuas were recorded. Since many of the chase victims were probably not breeding within the selected areas of cliff, these counts of arrivals did not indicate the total number of potential victims available to the skuas which were active in the area, but served as an index of the numbers available.

All observations were made with 10 by 50 binoculars. Chase durations were timed with a digital stopwatch. All observations were recorded on a portable cassette recorder and subsequently transcribed to notebooks. The local visibility during each observation period was obtained from meteorological data recorded at the weather station at the north end of the island.

2) Analyses of data

a) Aims of analyses

Analyses of the dataset were carried out with a view to answering several specific questions which are listed below:

1) Does the chase success rate differ between; light and melanic Arctic skuas, Arctic skuas and great skuas, skuas and gulls?

2) Have the success rates of light and melanic Arctic skuas changed over the years?

3) Are chases by groups of skuas more successful than chases by single skuas?

4) Is the formation of group attacks beneficial to both the initiator and the joiner?

5) Does the success rate of attackers in securing fish vary with the species of victim?

6) Do skuas exhibit any preference for a particular species of victim?

7) Do great skuas and Arctic skuas have different host preferences?

8) Have chase success rates changed since the mid 1970s?

9) Have host preferences changed since the mid 1970s?

10) Does the method of forcing victims to give up their fish, and the ability to secure fish dropped by victims, differ between light and melanic Arctic skuas, and between Arctic skuas and great skuas?

11) What factors differentiate between successful and unsuccessful chases by Arctic skuas and by great skuas?

12) Does the method of attack differ between light and melanic Arctic skuas and between Arctic skuas and great skuas?

b) Statistical techniques

The first ten questions above were investigated with the use of chi-square tests or Fisher's exact tests where sample sizes were small. However, the use of multivariate analyses was required in order to determine which of the many recorded variables best differentiated between successful and unsuccessful chases and to determine the ways in which the attack strategies employed by different phases/species of skua differed most. A pre-requisite of multiple regression analysis is that when using a dichotomous nominal dependent variable, the smaller of the two groups must contain at least 20% of the cases

(Hedderson 1987). Since this requirement was not always met by this dataset, it was decided that discriminant analysis was the most appropriate multivariate statistical technique to employ. Discriminant analyses were carried out by a stepwise selection method with maximisation of Rao's V as the criterion for variable selection. Variables were assumed to have made a significant contribution to the discriminant function if, when added to the equation, the probability of chance occurrence of the change in Rao's V was less than 0.05.

Unfortunately, a large number of cases had missing values for at least one of the independent variables used in the discriminant analyses. Consequently the discriminant equations were based on rather small subsamples of the dataset. In order to utilise a larger proportion of the cases in ultimately deriving the most important variables, an iterative procedure was employed.

When an initial discriminant analysis actually selected some of the variables available, the discriminant analysis was rerun with only those previously selected variables being used as the independent variables. If any of these variables were not re-selected, the process was repeated using only those variables which were re-selected. When all the variables were re-selected, only those which produced a significant change in Rao's V, when they were included in the equation, were selected for the next cycle. This process was repeated until all the independent variables available for selection were re-selected and gave a significant change in Rao's V when included in the

equation. In this way, the final discriminant equations were based on much larger proportions of the cases than would otherwise have been possible.

As a check of the validity of this technique, chi-square tests were carried out between the two groups of the dependent variable for each independent variable used in the discriminant analyses. These tests were based on a much higher proportion of the total number of cases than the discriminant analyses since cases were selected for each test regardless of whether they had missing values for any of the other variables. These tests served to identify any variables that might have been spuriously selected by the discriminant analyses or conversely any important variables which the discriminant analyses did not select.

c) Methods of Analysis

For the purposes of all analyses, a successful chase was, unless otherwise stated, defined as one in which a victim lost some or all of its fish as a result of the attack.

When appropriate, analyses were initially carried out on the largest number of chases possible by using chases of all species of victim together, and then repeated using only chases of puffins.

In the field, Arctic skuas were classified into three phases; light, intermediate or dark, in accordance with the classification scheme of O'Donald (1983). Inspection of the data revealed that whereas intermediate phase birds were more than twice as common as dark phase birds in the colony on Foula (Furness 1983, pers. obs.), the number of

chases recorded as having been by dark phase birds outnumbered those recorded as having been by intermediate phase birds. This suggested that many intermediate phase attackers had been mistakenly identified as dark phase, since misclassification was far more likely to have occurred when birds were involved in high speed chases than when sitting on their territories. In view of these findings, it was decided to reclassify chases by intermediate and so-called "dark" phase birds as having been by melanic individuals. Birds of light and "dark" phases were easily distinguished from one another without error.

At Foula, only three species of gulls (Family Laridae) were regularly seen patrolling at the observation sites. These were kittiwakes (Rissa tridactyla), common gulls (Larus canus) and herring gulls (Larus argentatus). None of these three species were ever present in large numbers, and those that were present tended to either join chases that were initiated by skuas or else to act as gleaners. Consequently, very few chases that were actually initiated by gulls, (which could serve as an indicator of their successfulness as kleptoparasites without the aid of skuas), were recorded in either 1986 or 1987. In order to increase the number of records of chases initiated by gulls, some observations were made in 1988. Even so, the number of chases by each of the three species of gull was still small. Thus, for comparison of the success rates of gulls, with those of skuas, chases by all three species of gull were combined.

Rather than compare the success rates of gulls with those of skuas for 1986, 1987 and 1988 separately, it was decided to combine data from the three years if there were no differences in success rates between the years. Unfortunately there were too few chases by gulls to test for differences in success rates between years. However, since the sample sizes for chases by skuas were much larger, it was decided that if the skuas' success rates did not differ significantly between years, then it was reasonable to assume that the same would be true for gulls, if larger samples sizes were available.

In order to determine whether skuas exhibited any degree of host preference, it was necessary to determine the proportions of different host species that were available to them. For each year, this was done by summing all the hourly counts of arrivals with fish. Since almost all the chases by great skuas were recorded at Kittiwakes' Haa and almost all the chases by Arctic skuas were recorded at Heddlicliff, host availability was determined separately for the two sites. Any chases by either species of skua which were recorded at the site normally frequented by the other, were excluded from these analyses of host preferences.

In 1986, the observations of Arctic skua kleptoparasitic behaviour began in the latter part of June. By this time, Arctic skuas do not chase Arctic terns (Sterna paradisaea) as frequently as they do prior to mid-June, (Furness 1980). The fact that no chases of Arctic terns were recorded in 1986 may reflect the late date on which observations were first made. It was, therefore, decided to omit the data from 1986

when examining changes in the host selection patterns of Arctic skuas.

Results

1) Comparison of success rates between attackers

a) Light and melanic Arctic skuas

There were no significant differences between the success rates of single light and melanic Arctic skuas, either against all species of victim combined or against any individual species of victim. This was true in both 1986 and 1987, (Tables 2.1 and 2.2). Similarly, the chase success rates of groups of Arctic skuas which included at least one light phase bird were not significantly different from those achieved by groups whose members were all melanic. Again this was true in both 1986 and 1987, (Tables 2.3 and 2.4).

b) Single skuas and groups of skuas

Since none of the above tests produced significant results, chases by single light phase and single melanic phase Arctic skuas were combined as were chases by groups of Arctic skuas, regardless of the phases of the group members. Comparison of the success rates of these two new groups showed that, in both years, chases by more than one Arctic skua were significantly more successful than chases by single skuas. This was true when considering all species of victim together and also puffins alone, (Tables 2.5 and 2.6). Investigation of the effect of group size on success rates against the other species of victim was severely influenced by the small numbers of chases by

groups of Arctic skuas. This was also the case for great skuas, (Tables 2.7 and 2.8). However, even when considering chases of all species of victim, and of puffins, the success rates of groups of great skuas did not differ significantly from those of single attackers, (Tables 2.7 and 2.8).

c) Great skuas and Arctic skuas

In both 1986 and 1987, solitary great skuas were significantly more successful than solitary Arctic skuas, against puffins, auks and all species of victim considered together, (Tables 2.9 and 2.10). In 1986, solitary great skuas were also more successful than solitary Arctic skuas, when chasing guillemots and razorbills, although only significantly so in the former. In 1987, solitary great skuas were again more successful than solitary Arctic skuas when chasing guillemots, but this result was not significant, nor was the difference in success rates between the two species when chasing razorbills. Groups of great skuas and groups of Arctic skuas did not differ significantly in their success rates against either puffins alone or all species of victim together. This was true in both 1986 and 1987, (Tables 2.11 and 2.12). Comparisons for other species of victim were hampered by small sample sizes.

d) Skuas and gulls

Neither Arctic skuas nor great skuas exhibited any significant differences between years 1986-1988 in their success rates against, either all species of victim together, ($X^2 = 0.75$, $p > 0.50$, $X^2 = 2.25$, $p > 0.10$ respectively), or against puffins alone ($X^2 = 1.35$, $p >$

0.50, X^2 = 1.83, p > 0.10 respectively). The overall success rates of both great skuas and Arctic skuas differed markedly from those of the gulls, (X^2 = 7.45, p < 0.005, X^2 = 3.04, p < 0.05 respectively). This was also the case when only chases of puffins were considered, (X^2 = 4.94, p < 0.025, X^2 = 1.69, p > 0.05). In this last comparison, which was not statistically significant due to small sample sizes, Arctic skuas were more than twice as successful as gulls, and such a large difference must surely be biologically important (Table 2.13).

2) Changes in the success rates of light and melanic Arctic skuas

Changes of the success rates of light and melanic phase Arctic skuas were studied by comparing data recorded on Foula in 1978 and 1979, with the data collected in 1986 and 1987, (Table 2.14). Against guillemots, the success rates of neither light nor melanic Arctic skuas differed significantly between 1978 and 1979, (p = 0.32 (Fisher's exact test), X^2 = 1.86, p > 0.10 respectively), or between 1986 and 1987, (X^2 = 0.02, p > 0.80, and X^2 = 0.09, p > 0.70 respectively). The success with which light and melanic Arctic skuas chased puffins did not differ significantly between 1978 and 1979, (X^2 = 0.30, p > 0.50 and X^2 = 0.16, p > 0.50 respectively), or between 1986 and 1987 (X^2 = 0.19, p > 0.50 and X^2 = 0.94, p > 0.30 respectively). Thus data from 1978 and 1979 were combined as were data from 1986 and 1987. The success rate of melanic Arctic skuas against puffins was significantly lower in 1986-87 than in 1978-79, (X^2 = 9.03, p < 0.01), but showed no statistically significant difference

between periods when chases of guillemots were considered (X^2 = 0.22, $p > 0.50$). The success rates of light phase Arctic skuas, against puffins and against guillemots, did not differ significantly between 1978-79 and 1986-87, (X^2 = 0.33, $p > 0.50$ and X^2 = 0.03, $p > 0.80$ respectively).

3) Profitability of group chases

In order to assess the profitability to attackers of forming groups, a successful chase was defined as one which resulted in one of the attackers securing a fish. In 1986 and 1987, the success rate of groups of two Arctic skuas was significantly higher than that of single attackers (X^2 = 4.12, $p = 0.04$ and X^2 = 5.16, $p = 0.02$ respectively), (Table 2.15). However, this was not the case for great skuas, (X^2 = 1.45, $p = 0.23$ in 1986 and X^2 = 0.06, $p = 0.81$ in 1987). In the case of Arctic skuas in 1986 and 1987, the success rate of the chase initiator did not differ significantly between chases which it carried out alone and those in which it was joined by another skua, (X^2 = 0.00, $p = 1.00$ in both years). This was also true for great skuas, (X^2 = 2.52, $p = 0.11$ in 1986 and X^2 = 1.26, $p = 0.26$ in 1987). Although the trend was not statistically significant, the success rate of the chase initiator tended to decrease if it was joined (Table 2.15).

4) Success rates against different species of victim

A successful chase was defined as one in which an attacker secured a fish. Only the three species of victim which were frequently chased (ie puffins, guillemots and razorbills) were used in these

analyses. Chases by more than one skua were included in these analyses in order to gain a measure of the overall success of skuas against each species of host, which might explain any tendency for skuas to select one species of host in preference to the others. The success rates of chases by Arctic skuas in 1986, differed significantly between the three species of auk, (X^2 = 6.69, p = 0.035), (Table 2.16). However, this was not true in 1987, (X^2 = 0.53, p = 0.769). The success rates of great skuas did not differ significantly between host species in 1986, (X^2 = 5.25, p = 0.073), or in 1987, (X^2 = 5.96, p = 0.051). The general trend was for puffins to be chased more successfully than razorbills which were in turn chased more successfully than guillemots.

5) Host selection in relation to availability

Arctic skuas selected victims in significantly different proportions to their availability in both 1986, (X^2 = 10.04, p < 0.01) and in 1987, (X^2 = 62.53, p < 0.001) The same was true for great skuas, (X^2 = 137.90, p < 0.001 in 1986 and X^2 = 100.02, p < 0.001 in 1987). Both species of skua showed a marked preference for chasing puffins (Table 2.17).

6) Differences in the host preferences of Arctic skuas and great skuas

In both 1986 and 1987, Arctic skuas and great skuas differed significantly in terms of their host selection patterns, (X^2 = 279.12, p < 0.001 and X^2 = 109.47, p < 0.001 respectively), (Table 2.17). In both years, Arctic skuas chased a higher proportion of puffins and

razorbills and a lower proportion of guillemots than great skuas. This pattern was mirrored exactly in the different proportions of the three species of auk available to the two species of skua, which also differed significantly in 1986, (X^2 = 695.81, $p < 0.001$) and in 1987, (X^2 = 396.25, $p < 0.001$), (Table 2.17).

7) Comparison of success rates between years

The success rate of chases of puffins by Arctic skuas, varied significantly between the years of 1975-76, 1978, 1979, 1980, 1986 and 1987, (X^2 = 17.92, $p < 0.01$) ,(Table 2.18). Since the success rate of Arctic skuas against puffins did not differ significantly between years when 1986 and 1987 were excluded, (X^2 = 5.62, $p > 0.10$), or between 1986 and 1987, (X^2 = 0.54, $p > 0.30$), data collected between 1975 and 1980 were combined as were the data of 1986 and 1987. The success rate of chases of puffins by Arctic skuas was significantly lower in the last two years than it was previously, (X^2 = 10.73, $p < 0.01$). The same pattern was seen when the success rate of great skuas against puffins was studied. The success rate achieved by great skuas when chasing puffins did not differ significantly between 1986 and 1987, (X^2 = 1.80, $p > 0.10$), but was significantly lower in 1986-87 than in 1975-76, (X^2 = 6.40, $p < 0.02$).

Between years, the success rates of Arctic skuas against guillemots and against razorbills did not differ significantly, (X^2 = 6.34, $p > 0.20$ and X^2 = 4.61, $p > 0.05$ respectively). The same was true for great skuas, (X^2 = 4.42, $p > 0.10$ for guillemots and X^2 = 1.17, $p > 0.50$ for razorbills). The success rate of great skuas against gannets,

(Sula bassana), did not differ significantly between years, (X^2 = 4.56, $p > 0.10$). The success rate of Arctic skuas against Arctic terns differed significantly between years, (X^2 = 24.14, $p < 0.001$). However, this was still the case, even when the data from 1987 were excluded, (X^2 = 18.54, $p < 0.001$).

8) Changes in host preference between years

The proportions of the various species of victim chased by great skuas differed significantly between the years 1975-76,1986 and 1987, (X^2 = 67.30, $p < 0.001$), (Table 2.19). Because there was a significant difference in this respect between 1986 and 1987, (X^2 = 17.21, $p < 0.01$), these two years were next compared separately with 1975-76. In both cases, the results were significant, (X^2 = 63.56, $p < 0.001$, for the comparison with 1986, and X^2 = 17.01, $p < 0.01$, for the comparison with 1987). The major differences were that in both 1986 and 1987, the proportion of chases of gannets was lower than in 1975-76, while the proportion of chases of guillemots was higher, and the proportion of chases of puffins was lower in 1987 than in 1975-76.

The host selection patterns of Arctic skuas differed significantly between the years 1975-76, 1978, 1979 and 1987, (X^2 = 651.31, $p < 0.001$). There were also significant differences in the host selection patterns of Arctic skuas between the years of good tern breeding success, ie 1975-76 and 1979, (X^2 = 51.61, $p < 0.001$), and between the years of poor tern breeding success, ie 1978 and 1987, (X^2 = 45.65, $p < 0.001$). In 1979, Arctic terns were chased less frequently than in

1975-76 while puffins and guillemots were chased more frequently. In 1987, terns were chased less often than in 1978 while razorbills were chased more frequently.

9) Methods of obtaining fish and efficiency at obtaining dropped fish

a) Light phase and melanic phase Arctic skuas

In 1986, light and melanic Arctic skuas did not differ significantly in how they forced their victims to release their fish, either when all victims were considered, (X^2 = 0.86, p = 0.652), or when only puffins were considered, (X^2 = 0.14, p = 0.933), (Table 2.20). The same was true in 1987, (X^2 = 6.05, p = 0.05, when all victims were considered, and X^2 = 4.61, p = 0.100, for chases of puffins), (Table 2.21). The overall ability of light and melanic Arctic skuas to secure dropped fish did not differ significantly in either 1986, (X^2 = 1.87, p = 0.172), (Table 2.20), or in 1987, (X^2 = 0.00, p = 1.00), (Table 2.21). The same was true when only chases of puffins were considered, (X^2 = 2.12, p = 0.146 in 1986 and X^2 = 0.21, p = 0.647 in 1987). Similarly, light and melanic Arctic skuas did not differ significantly in their overall ability to secure fish from the sea-surface in 1986, (X^2 = 0.05, p = 0.827), (Table 2.20), or in 1987, (X^2 = 1.42, p = 0.234), (Table 2.21). The same was also true when only chases of puffins were considered, (X^2 = 0.79, p = 0.373 in 1986 and X^2 = 2.67, p = 0.102 in 1987).

In 1986, when chases of all victims were considered, light Arctic skuas secured a significantly higher proportion of their fish in the air than did melanics, (X^2 = 6.14, p = 0.013), (Table 2.20). This was

not the case in 1987, (X^2 = 0.51, p = 0.475),(Table 2.21), or in either year, when only chases of puffins were considered, (X^2 = 0.29, p = 0.593 in 1986 and p = 0.455 (Fisher's exact test) in 1987).

b) Arctic skuas and great skuas

When chases of all victims in 1986 were considered, Arctic skuas and great skuas were found to differ significantly in how they caused their victims to release their fish, (X^2 = 49.51, p < 0.0001), (Table 2.20). This was also true in 1987, (X^2 = 16.59, p = 0.0003), (Table 2.21). When only chases of puffins were considered, the situation was again the same in both 1986, (X^2 = 30.57, p < 0.0001), (Table 2.20), and in 1987, (X^2 = 13.00, p = 0.0015), (Table 2.21). In all these comparisons, the victims of Arctic skuas were far more likely to have had their fish stolen directly from their bills than were the victims of great skuas.

In 1986, Arctic skuas secured a significantly lower proportion of the fish that were dropped by all of their victims, than did great skuas, (X^2 = 14.00, p = 0.0002), (Table 2.20). This was also true in 1987, (X^2 = 5.18, p = 0.023), (Table 2.21). When only chases of puffins were considered, this same situation occurred in 1986, (X^2 = 13.99, p = 0.0002), (Table 2.20), and in 1987, (X^2 = 6.85, p = 0.009), (Table 2.21).

Arctic skuas and great skuas did not differ significantly in their overall ability to secure fish from the sea-surface in either 1986, (X^2 = 0.13, p = 0.715), (Table 2.20), or in 1987, (X^2 = 2.89, p =

0.089), (Table 2.21). Similarly when the fish were lost by puffins, great skuas and Arctic skuas did not differ significantly in their ability to secure them from the sea-surface, either in 1986, (X^2 = 1.13, p = 0.289), (Table 2.20), or in 1987, (X^2 = 1.48, p = 0.224), (Table 2.21).

When chases of all victims in 1986 were considered, great skuas did not differ significantly, in terms of the proportion of successful chases in which they secured fish in the air, from light phase Arctic skuas , (X^2 = 2.67, p = 0.102), melanic Arctic skuas, (X^2 = 1.53, p = 0.216), or all Arctic skuas together, (X^2 = 0.00, p = 1.000), (Table 2.20). However, in 1987, this was not the case, for great skuas secured a significantly lower proportion of their fish in the air than did Arctic skuas, (X^2 = 7.32, p = 0.007), (Table 2.21). When only chases of puffins were considered, great skuas and Arctic skuas did not differ significantly in this respect in either 1986, (X^2 = 0.00, p = 1.000), (Table 2.20), or in 1987, (X^2 = 3.69, p = 0.055), (Table 2.21).

In those comparisons which revealed that Arctic skuas and great skuas differed significantly in their ability to secure dropped fish, but not in their ability to secure fish from the sea surface, their ability to secure fish in the air was compared.

Great skuas and Arctic skuas did not differ significantly in their overall ability to secure fish in the air in either 1986, (X^2 = 0.88, p > 0.30), (Table 2.22), or in 1987, (X^2 = 1.33, p > 0.20), (Table 2.22). When only chases of puffins were considered, again great skuas

and Arctic skuas did not differ significantly in this respect in either 1986, (X^2 = 0.71, p > 0.30), (Table 2.22), or in 1987, (X^2 = 0.36, p > 0.50), (Table 2.22).

In 1986, the fish dropped by the victims of Arctic skuas, landed significantly more often on the rocks than did fish dropped by the victims of great skuas, (X^2 = 38.44, p < 0.001), (Table 2.23). This was also true in 1987, (X^2 = 9.37, p < 0.01), (Table 2.23). Even fish dropped by puffins which were chased by Arctic skuas, landed significantly more often on the rocks than fish dropped by puffins chased by great skuas. Again this was true in both 1986, (X^2 = 21.45, p < 0.001), and in 1987, (X^2 = 6.52, p < 0.02), (Table 2.23).

In all cases, the ability of Arctic skuas to secure dropped fish was significantly lower if the fish landed on the rocks rather than on the sea surface, (X^2 = 35.55, p < 0.001 for chases of all victims in 1986, X^2 = 30.15, p <0.001 for chases of puffins in 1986, p = 0.016 for chases of all victims in 1987 (Fisher's exact test), and p = 0.009 for chases of puffins only in 1987 (Fisher's exact test)), (Table 2.23).

10) Differences between successful and unsuccessful chases

Against all species of victim, chases by great skuas were more likely to be successful if; the speed of reaction of the victim was slow, (Rao's v = 9.33, p = 0.002), the victim was high above the water when the chase began, (change in Rao's V = 8.91, p = 0.003) and if the local visibility was poor, (change in Rao's V = 4.06, p = 0.044), (Table 2.24). This last variable did not differ significantly between

successful and unsuccesful chases when analysed by the chi-square tests, (X^2 = 0.60, p = 0.896), (Table 2.25). Given this result and the only marginal significance of average visibility as a discriminating variable, it is unlikely that the effect of visibility on success is very pronounced. The chi-square tests did reveal that chases by great skuas were more likely to be successful if; the attacker approached to within 1m of the victim, (X^2 = 19.90, p < 0.001), and if the attacker made contact with the victim, (X^2 = 18.28, p < 0.001). These two variables were very closely related to one another.

Chases of puffins by great skuas were more likely to be successful if the victim was high above the water at the start of the chase, (Rao's V = 7.62, p = 0.006), (Table 2.24). The chi-square tests also showed that chases of puffins were more likely to be successful if the speed of reaction of the victim was slow, (X^2 = 9.63, p = 0.008), (Table 2.26).

Against all victims, chases by Arctic skuas were more likely to be successful if; the skua approached to within 1m of the victim, (Rao's V = 14.73, p < 0.001), the chase was towards the cliff, (change in Rao's V = 6.82, p = 0.009), the victim was high above the water when the chase began, (change in Rao's V = 4.13, p = 0.042) and the attacker initiated the chase with descending flight, (change in Rao's V = 6.55, p = 0.011), (Table 2.24). The last of these variables was not significantly different between successful and unsuccessful chases when analysed by the chi-square tests, (X^2 = 2.89, p = 0.236), (Table 2.27). However, the chi-square tests indicated that chases by Arctic

skuas were also more likely to be successful if; the speed of reaction of the victim was slow, (X^2 = 37.66, $p < 0.001$), the skua approached to within 1m of the victim, (X^2 = 72.49, $p < 0.001$), the skua made contact with the victim, (X^2 = 77.72, $p < 0.001$), the skua made rapid turns during the chase, (X^2 = 21.23, $p < 0.001$) and the longer the chase continued, (X^2 = 15.66, $p = 0.001$), (Table 2.27).

Chases of puffins by Arctic skuas were more likely to be successful if; the skua approached to within 1m of the victim, (Rao's V = 13.33, $p < 0.001$), the chase was towards the cliff, (change in Rao's V = 11.98, $p < 0.001$), the attacker initiated the chase with descending flight, (change in Rao's V = 5.35, $p = 0.021$), the victim was high above the water when the chase began, (change in Rao's V = 5.27, $p = 0.022$), and the chase was late in the season, (change in Rao's V = 5.63, $p = 0.018$), (Table 2.24). The last two variables were, however, not significantly different between successful and unsuccessful chases when analysed by chi-square tests, (X^2 = 3.36, $p = 0.186$ and X^2 = 13.42, $p = 0.144$ respectively), (Table 2.28). This implied that the influence of these two variables on the outcome of chases was marginal. The chi-square tests indicated that chases of puffins by Arctic skuas were also more likely to be successful if; the speed of reaction of the victim was slow, (X^2 = 36.07, $p < 0.001$), the attacker made contact with the victim, (X^2 = 62.61, $p < 0.001$), the skua made rapid turns during the chase, (X^2 = 19.75, $p < 0.001$), the attacker used flapping flight during the chase, (X^2 = 5.21, $p = 0.022$), the

victim was near the cliff when the chase began, (X^2 = 16.80, $p < 0.001$), and the longer the chase continued, (X^2 = 11.00, p = 0.012), (Table 2.28).

All the variables which were selected by the discriminant analyses as being of importance in discriminating between successful and unsuccessful chases, were found to differ significantly between these two categories, by means of the chi-square tests, with the few exceptions mentioned above.

11) Differences between attack strategies

a) Light and melanic phase Arctic skuas

Overall, light phase birds were more likely than melanic phase birds, to initiate their chases with level or ascending flight, (Rao's V = 12.86, $p < 0.001$), and also to continue their chases for longer, (change in Rao's V = 6.49, p = 0.011), (Table 2.29). These results were supported by the chi-square tests, (Table 2.30), which also showed that the victims of light phase birds were less likely to have been low over the water when the chase began, (X^2 = 16.88, $p < 0.001$). As a consequence of this, light phase birds initiated a significantly higher proportion of their chases from the same height as, or from below their victim, (X^2 = 8.78, p = 0.012). The speed of reaction of the victims was less likely to be fast to light phase birds than to melanic phase individuals, (X^2 = 7.07, p = 0.029), (Table 2.30).

When puffins were the victims, light phase birds were again more likely to have initiated their chases with level or ascending flight than melanic birds, (Rao's V = 8.05, p = 0.005), (Table 2.29). Again

the chi-square tests supported this finding and also indicated that puffins chased by light phase skuas were less likely to have been low over the water when the chase began, (X^2 = 15.17, $p < 0.001$). Hence chases of puffins by light phase skuas were more likely to have been initiated from the same height or below the victim than chases by melanics, (X^2 = 9.48, $p = 0.009$). The speed of reaction of puffins was less likely to have been fast when attacked by light phase skuas, (X^2 = 8.31, $p = 0.016$). Chases by light phase skuas tended to continue longer than chases by melanic phase birds, (X^2 = 12.86, $p = 0.005$), (Table 2.31).

b) Arctic skuas and great skuas

Overall, chases by Arctic skuas were, in comparison with those by great skuas, more likely to have; been initiated from in front of the victim, (Rao's V = 105.98, $p < 0.001$), resulted in the attacker approaching to within 1m of the victim, (change in Rao's V = 33.07, $p < 0.001$), been initiated from the same height as or below the victim, (change in Rao's V = 27.13, $p < 0.001$), been initiated without a swoop from above on closed wings, (change in Rao's V = 20.03, $p < 0.001$), continued longer, (change in Rao's V = 19.18, $p < 0.001$), and involved rapid agile turns, (change in Rao's V = 4.30, $p = 0.038$), (Table 2.29). The chi-square tests supported all of these results, (Table 2.32). In addition, the chi-square tests indicated that Arctic skuas were significantly more likely than great skuas to; have initiated their chases with level or ascending flight, (X^2 = 106.49, $p < 0.001$),

have used flapping flight during their chases, (X^2 = 214.97, $p < 0.001$), have chased low flying victims, (X^2 = 20.56, $p < 0.001$). The speeds of reaction of the victims were significantly faster to great skuas than to Arctic skuas, (X^2 = 67.74, $p < 0.001$). Arctic skuas made contact with their victims significantly more often than great skuas, (X^2 = 55.54, $p < 0.001$). Chases by Arctic skuas were significantly more likely to be parallel to the cliff than chases by great skuas, (X^2 = 19.28, $p < 0.001$) and significantly less likely to result in the victim landing on or diving into the sea, (X^2 = 10.92, $p = 0.001$), (Table 2.32).

Chases of puffins by Arctic skuas were, in comparison with those by great skuas, more likely to have; resulted in the attacker approaching to within 1m of the victim, (Rao's V = 83.23, $p < 0.001$), been initiated without a stoop from above, (change in Rao's V = 46.47, $p < 0.001$), been of low-flying victims, (change in Rao's V = 31.36, $p < 0.001$), been initiated from the same height as, or below the victim, (change in Rao's V = 25.75, $p < 0.001$), involved flapping flight by the attacker, (change in Rao's V = 18.83, $p < 0.001$), resulted in a slow speed of reaction from the victim, (change in Rao's V = 22.48, $p < 0.001$), been towards the cliff, (change in Rao's V = 17.01, $p < 0.001$), and to have continued for a long time, (change in Rao's V = 4.57, $p = 0.033$), (Table 2.29). The chi-square tests supported all of these results, (Table 2.33). In addition, the chi-square tests indicated that Arctic skuas were more likely than great skuas to have initiated their chases from the side of or in front of the victim, (X^2

= 94.67, $p < 0.001$), and used level or ascending flight in the process, (X^2 = 47.95, $p < 0.001$). Also, chases by Arctic skuas involved rapid turns significantly more often than those by great skuas, (X^2 = 71.97, $p < 0.001$), and more often resulted in the attacker making contact with the victim, (X^2 = 58.82, $p < 0.001$). Arctic skuas chased puffins parallel to the cliff significantly more often than great skuas, (X^2 = 13.45, $p < 0.001$), but chased them away from the cliff significantly less often than great skuas, (X^2 = 36.16, $p < 0.001$), (Table 2.33).

12) Speed of reaction to light and melanic Arctic skuas in relation to the height of the attacker

The speed of reaction of victims to approaching light and melanic Arctic skuas did not differ significantly when the attacks were initiated from above the victim, (X^2 = 2.72, $p = 0.257$ for all victims and X^2 = 4.88, $p = 0.087$ for puffins only). This was also true when attacks were initiated from the same height as the victim, (X^2 = 0.50, $p = 0.778$ for all victims and X^2 = 0.58, $p = 0.748$ for puffins only) and when initiated from below, (X^2 = 0.76, $p = 0.684$ for all victims and X^2 = 0.55, $p = 0.758$ for puffins only), (Table 2.34). The victims' speed of reaction to attacking melanic Arctic skuas differed significantly between chases which were initiated from above, the same height or below, (X^2 = 29.36, $p < 0.001$), (Table 2.34). This was not the case when victims were attacked by light phase Arctic skuas, (X^2 = 6.46, $p = 0.168$), although the trends were similar. The same pattern

was evident when only chases of puffins were considered (X^2 = 17.10, p = 0.002 for chases by melanic birds and X^2 = 1.56, p = 0.816 for chases by light phase birds).

13) Success rates of light and melanic phase Arctic skuas in relation to the height of the attacker

Chases of all victims by light phase Arctic skuas were significantly more likely to be successful if the attacker initiated the chase from above or from the same height as the victim rather than from below, (X^2 = 7.39, p = 0.025), (Table 2.35). This was not the case when melanic Arctic skuas were the attackers, (X^2 = 5.25, p = 0.072), (Table 2.35). Chases of puffins by light phase Arctic skuas were also significantly more likely to be successful if initiated from above or the same height as the victim, rather than when initiated from below, (X^2 = 8.27, p = 0.016), (Table 2.35). Again, this was not the case when melanic Arctic skuas were the attackers, (X^2 = 3.60, p = 0.166), (Table 2.35).

Discussion

1) Apostatic selection, aggressive camouflage and the success rates of light and melanic phase Arctic skuas

Although seabirds are generally less colourful than landbirds, there is still considerable variation in patterns of plumage colouration between species (Simmons 1972, Nelson 1980). It has been suggested that the the three main categories of plumage patterns found among seabirds are at least partly related to feeding techniques (Simmons

1972). Andersson (1976) suggested that the dark plumage of Arctic skuas which feed by kleptoparasitism could be a form of aggressive camouflage to make them less conspicuous to their victims. Furness (1987b) suggested that the dark plumage of skuas of the genus Catharacta and of frigatebirds may also be cryptic. However, Nelson (1980) considered that "all-black plumage is, so far, relegated to the dust-bin of 'special pleading'", and that "there is no convincing interpretation" for such plumage colouration.

The reasons underlying the marked plumage polymorphism of Arctic skuas have been the subject of much debate, and several different theories exist to explain its occurrence (O'Donald and Davis 1959, Paulson 1973, Arnason 1978, Furness and Furness 1980, O'Donald 1983, Rohwer 1983, Furness 1987a). Furness (1987a) discussed the major theories which have been proposed to explain the maintenance of the plumage polymorphism of Arctic skuas; the occurrence of assortative mating and sexual selection, the timing of breeding hypothesis, the heat-loss hypothesis, the aggressive camouflage hypothesis and the apostatic selection hypothesis.

According to the theory of apostatic selection, as originally proposed by Paulson (1973), the success rate of the rarer phase in a population, should be higher than that of the more common phase. On the island of Foula, Shetland, light phase Arctic skuas comprised 23.4% of the population in 1986, (Ewins et al. 1986). Light phase Arctic skuas were, therefore, the rarer of the two phases in the Foula

population. Thus in this case it would be expected that, if the apostatic selection hypothesis were true, light phase birds would have higher success rates than melanic phase birds.

Since in no case was the success rate of single light phase birds significantly higher than that of single melanic birds, the results of this study do not support the apostatic selection theory. Moreover, the success rate of groups of Arctic skuas of which at least one was a light phase individual was in no case significantly higher than that enjoyed by groups of which all the members were melanic. Both these results are totally contrary to those of Arnason (1978), and consequently are in accord with those of Furness and Furness (1980). Furness and Furness (1980), pointed out that if the predictions of the theory of apostatic selection are taken in conjunction with the idea that melanic individuals have an advantage over light phase individuals in terms of their greater crypticity against sea-cliffs (Andersson 1976), then in Shetland it would be expected that the success rates of the two phases will be similar.

Rohwer (1983), stated that the prediction of Paulson (1973), that the rarer morph in a population will always have a higher success rate than the more common morph, is valid under only two conditions. These conditions are that either; 1) both morphs are equally easy for prey to perceive, (as assumed by Arnason (1978)), or if they are not, (as suggested by Furness and Furness (1980)),then 2) the rare morph must be held below the equilibrium frequency that would be achieved solely by apostatic selection because of some disadvantage it suffers outside

of interactions with prey. Rohwer (1983), further pointed out that if the two morphs in a population are at or near their equilibrium frequency and non-foraging aspects of fitness are unrelated to colour, then the success of individuals of one phase should be very similar to that of individuals of the other phase. Thus, as noted by Rohwer (1983), the contradictory results of Arnason (1978) and of Furness and Furness (1980), are both compatible with the apostatic (or avoidance-image) hypothesis, depending on whether or not the population under study had reached its equilibrium frequency.

As an experimental field test of the apostatic selection hypothesis, Rohwer (1983), suggested that the relative success rates of individuals of the two morphs in a population could be compared before and after their relative frequencies were altered by removals. No such removals were made during this study. However, over the last few years, natural processes have produced the result that would have been achieved by such removals. The proportion of light phase Arctic skuas in the Foula population was 29.9% in 1975, (Davis and O'Donald 1976), and has now declined to 23.4%, (Ewins et al. 1986). If the apostatic selection hypothesis is true then the success rates of the remaining light phase birds should be higher than before while those of the now more common melanic birds should be lower, (Rohwer 1983). On the whole, these predictions seem to be upheld by the data, (Table 2.14), although only in one case was the difference statistically significant. Perhaps the decline in the proportion of light phase

birds on the island has not been large enough to produce readily detectable changes in the success rates of the two phases. Perhaps if the proportion of light phase birds on Foula declines further in the future, comparison of success rates with those of the past will yield significant changes. In addition, as pointed out by Rohwer (1983), any such changes over time might be expected to occur slowly if the majority of potential victims have already been attacked by individuals of both phases. Since auks are generally long-lived (Nettleship and Birkhead 1985), this is likely to be the case in this situation. Perhaps as the proportion of breeding auks which consists of individuals that bred when light phase birds were more common (and which are more likely to have an "avoidance image" for light phase birds) declines due to mortality of old birds, the success rate of light phase birds will increase further relative to that of melanic birds.

Rohwer (1983) summarised the predictions of the avoidance-image hypothesis as follows: "In short, the formation of avoidance-images is hypothesised to cause prey more strongly to avoid hawks similar in colour to those that have attacked them previously than other hawks whose colouration is novel". If, as seems reasonable, the word "rapidly" is substituted for "strongly" in this sentence, it becomes clear why, if the theory were true, individuals of the rare morph in a population could enjoy a higher success rate than individuals of the common morph. If victims take evasive action as soon as they realise that they are being attacked, it seems obvious that if victims

perceive the more common morph of attacker more rapidly than the rarer morph, because they have a search-image for the former, they should take evasive action sooner, and presumably escape more often, when attacked by a member of the more common morph.

In accordance with their findings in connection with the success rates of light and melanic Arctic skuas, Furness and Furness (1980), found no significant differences in the speeds of reaction of the host species to light and melanic phase attackers. However, in this study the speed of reaction of all species of victim alike and of puffins alone was significantly less likely to be fast when they were attacked by light phase Arctic skuas than by melanic Arctic skuas (Tables 2.30 and 2.31). A more detailed examination of these results revealed that victims were also marginally less likely to respond slowly when attacked by light phase Arctic skuas than by melanic phase individuals. Obviously there is no clear trend in these results and the statistical significance of the chi-square tests is considered to be a statistical anomaly due to the use of three categories for this variable, rather than two. The fact that "speed of reaction" was not selected by the discriminant analyses as an important discriminating variable between chases by light and melanic Arctic skuas (Table 2.29) lends support to this conclusion. One complication with both of these analyses is that while Arctic skuas initiate chases from above, below and the same height as their victims, the only chases in which the two phases will appear different to the victim under attack is when the

skuas attack from above, since the dorsal surfaces of the two phases are identical. Therefore, a more appropriate test of the apostatic selection hypothesis than the ones discussed immediately above, would be to compare the speed of reaction of victims to their attackers once the latters' initial height relative to that of the former has been controlled for. If speed of reaction to the two phases differs at all, it should only do so in chases which are initiated from above. This prediction is partly supported by the finding that the victims' speeds of reaction did not differ significantly between the two phases of attacker when the latter attacked from below or from the same height as the victim (Table 2.34). However, since this was also true when the Arctic skuas attacked their victims from above (Table 2.34), these more detailed analyses of victims' speeds of reaction would appear to lend no support to the apostatic selection hypothesis. However, for the reasons given previously, even this result cannot be considered to positively refute the validity of the avoidance-image hypothesis.

Paulson (1973), suggested that one line of evidence for a causal relationship between apostatic selection and polymorphism in vertebrate predators is the fact that "polymorphism in hawks is almost always a characteristic of the ventral surface, the surface the prey would most likely see when the hawk was a threat to it". Like polymorphic hawks the polymorphism of Arctic skuas is expressed ventrally, and since both phases of Arctic skua begin more than half of their attacks from above their targets, it is this surface which their victims will see most often. Presumably skuas prefer to attack

from above because chases in which gravity can be used to gain speed are considerably more cost effective than those in which they have to accelerate in level or even ascending flight. This would be particularly true if the expectation of success was no greater when attacking from the same height or below a victim, than when attacking from above. It is, therefore, extremely interesting that while light phase Arctic skuas were almost three times as successful when they attacked from above than from below while melanics were not, that it was light phase birds which initiated more chases with level or ascending flight from the same height or below their intended targets. This result poses at least three questions: 1) Why were light phase Arctic skuas three times more successful when attacking from above than when attacking from below, particularly when melanic Arctic skuas were not? 2) Why were light phase Arctic skuas nearly twice as successful as melanic phase Arctic skuas when attacking from above, but only about half as successful as melanics when attacking from below? 3) Given the relative success rates of light phase and melanic phase Arctic skuas when attacking from above and below, why was it the light phase birds which initiated a lower proportion of their chases from above their victims?

One possible explanation for these anomalous results lies in the marked reversed sexual size dimorphism of Arctic skuas (Andersson and Norberg 1981, Furness 1987a) , and the differences in the proportion of males and females that are light as opposed to melanic. Female

Arctic skuas weigh approximately 16.5% more than males (Furness 1987a) and approximately 70% of light phase birds on Foula, are females (Furness 1987a). This means that the average light phase bird has a higher mass than the average melanic phase individual. When descending towards their victims from above, the heavier light phase birds might gain more momentum than melanic phase birds. Thus light phase birds might represent more of a potential threat of injury to victims, which might be more willing to release their fish as a result. On the other hand when attacking from below the heavier light phase birds might be at a disadvantage both in relation to when they themselves attack from above, and relative to the melanic phase birds which, being smaller on average, should have more excess power available for climbing and hence be capable of more rapid rates of climb (Pennycuick 1975). However, any such differences between the phases of the Arctic skuas are likely to be slight and even if these tenuous theories can answer the first two questions given above, it remains difficult to see why the light phase birds initiated fewer chases from above their victims than the melanic phase individuals.

It is extremely interesting that frigatebirds (Family Fregatidae), the only group of birds which are more closely associated with kleptoparasitism than skuas, also exhibit reversed sexual size dimorphism (Cramp and Simmons 1977) and plumage polymorphism that is expressed ventrally (Harrison 1983). Female frigatebirds are heavier than males of the same species and in all species, except the Ascension frigatebird (Fregata aquila), show patches of pale coloured

plumage on their underparts which adult males do not. The similarity between these trends and those which exist among Arctic skuas in Shetland merits investigation in view of the fact that frigatebirds and Arctic skuas are among the most highly kleptoparasitic of all birds.

2) Differences in success rates between Arctic skuas and great skuas

Brockman and Barnard (1979) suggested that in many kleptoparasitic associations, the victim may surrender its food to a pursuer as a form of anti-predator behaviour in order to make good an escape while the attacker attempts to obtain the food. If this is indeed the case then it would seem reasonable to expect that the greater the potential threat posed by an attacker, the more likely a victim would be to release its fish.

Although great skuas in Shetland feed predominantly on sandeels (Ammodytes marinus) and whitefish discards from fishing boats (Furness and Hislop 1981, Hudson 1986, Furness 1987a, Hudson and Furness 1988) they are very capable of preying on adult seabirds. Predatory feeding by great skuas is well documented, (Bayes,Dawson and Potts 1964, Furness 1987a). Occasionally, victims of kleptoparasitic chases by great skuas are killed (pers.obs.). There seem to be no records, however, of Arctic skuas preying on adult auks during the breeding season. Presumably this reflects the relatively small size of Arctic skuas. Since great skuas are obviously much more of a threat to auks it is not surprising that the success rate of solitary great skuas in

inducing their victims to drop their fish was almost invariably higher than that achieved by Arctic skuas, (Tables 2.9 & 2.10). These results agree with those of Hulsman (1976) who found that the likelihood of success of the kleptoparasite which he was studying was higher, the smaller the victim in relation to the size of the attacker.

3) The profitability of group attacks

Foraging-group size is a key aspect of foraging strategies (Schoener 1971); the extremely wide range of foraging-group sizes found in nature bears testimony to this fact. Foraging-group sizes can vary seasonally within species, for example many species of bird such as the knot (Calidris canutus) which are solitary and territorial when breeding, form large feeding flocks during the non-breeding season (Cramp and Simmons 1983). Foraging-group sizes also vary between species and tend to reflect the feeding techniques employed; birds which are raptorial tend to hunt solitarily (Newton 1986) while flock feeding is beneficial to many species, for example piscivorous birds which sometimes use "group drives" to catch prey (Emlen and Ambrose 1970).

The effect of the number of attackers on the likely outcome of kleptoparasitic chases has been studied by many authors, (Hatch 1970,1975, Grant 1971, Hopkins and Wiley 1972, Andersson 1976, Hulsman 1976, Arnason 1978, Arnason and Grant 1978, Furness 1978a, Taylor 1979). In all of these studies, the likelihood of the victim dropping its fish increased with the number of attackers.

Where sample sizes for group attacks by Arctic skuas were large enough, the same trend was apparent in the results of this study (Tables 2.5 and 2.6). Arnason and Grant (1978) suggested that one reason for this could be that victims which change direction during a chase, are more likely to be intercepted by an attacker which "cuts the corner" if there is more than one attacker in pursuit. In contrast, however, chases by groups of more than one great skua were, in no instance significantly more successful than chases by solitary attackers (Tables 2.7 & 2.8). This latter result is somewhat surprising given the results for Arctic skuas in this study and the results of the studies listed above. Andersson (1976) and Furness (1978a) found that chases of gannets by groups of great skuas were significantly more successful than chases by solitary birds. That this was not the case in the present study probably reflects the very small number of group chases of gannets recorded. Maxson and Bernstein (1982) found that the success rate achieved by groups of South polar skuas (Catharacta maccormicki) chasing solitary blue-eyed shags (Phalacrocorax atriceps) was no higher than that achieved by solitary attackers. Furness (1978a) found that the number of great skuas chasing puffins did not influence the likelihood of success, as was the case in the present study. It would appear that, at least for great skuas, the effect of group size on the likelihood of success depends on what they are chasing.

Given that in most cases, the formation of groups by kleptoparasites increases the likelihood of the victim releasing its fish, this stategy seems, at first sight, to be a profitable one to the kleptoparasites. However, when the yield per attacker is considered only Hatch (1970), Grant (1971), Hulsman (1976), and Taylor (1979) found that the success rate achieved by groups was sufficiently higher than that achieved by singletons to result in a greater yield per bird for attackers that chased in groups. In the other studies listed above, the yield per bird was lower for birds that chased in groups than for birds which chased alone. Further, Hatch (1975) found that in chases by groups of laughing gulls (Larus atricilla), the success of the bird which initiated the chase was lower than that of the average group member. This led Hatch (1975) to propose that group chases by laughing gulls were an example of a selfish group. Although victims of chases by groups of Arctic skuas were significantly more likely to drop their fish than when chased by single Arctic skuas, only in the case of Arctic skuas in 1987 was the success rate in securing fish more than twice as high when two skuas attacked as when one did so. Hence only in this case could this strategy be of benefit to both attackers. However, even in this instance, the yield to the initiator of the chase was lower, although not significantly so, when it was joined by another attacker than when it chased alone. The same was true for great skuas in 1986 and 1987, while in 1986, initiators of Arctic skua chases seemed to gain no benefit from being joined. Since chase initiators did not benefit from being joined, as found by Hatch

(1975), it is clear that group chases occurred only because it was of benefit to the joiner to join even if the yield per bird of multiple chases was lower than that of chases by single skuas. Taylor (1979) pointed out that it is not essential that a bird should experience an increase in success rate for group chases to develop, only that the bird should do better than if it had continued to patrol and/or chase on its own during the period of the group chase. Given that for each chase the success rate per bird was higher in chases by single skuas than in chases by more than one skua, it seems reasonable to suggest that the reason why joiners joined initiators was that it was more profitable to join a chase than to continue patrolling. The results of this study are, in general, in accord with those of Hatch (1975), which leads to the conclusion that kleptoparasitic association between skuas is another example of a selfish group.

4) Success rates of specialist and opportunist kleptoparasites

One of the major arguments against the division of kleptoparasites into "specialists" and "opportunists" (Brockman and Barnard 1979) is that, contrary to all expectations, the so-called "specialist" kleptoparasites seem to be no more successful in inducing their victims to drop their fish, than are so-called "opportunist" kleptoparasites (Furness 1987b).

One problem in comparing success rates of different species from different studies, is the effect that the topography of the study site can have on the success rates recorded. For example, Arnason (1978)

recorded a success rate of 63.4% for chases of puffins by single Arctic skuas in Iceland, while on Foula, the comparable figures were 19.6% in 1986 and 16.9% in 1987. This large difference in success rates between colonies can be attributed to the fact that one of the main escape responses of puffins is to descend to the sea-surface where they have the option of diving to safety should the skua approach too closely. At the Iceland colony, this option was not open to the puffins, as the breeding cliff was, unlike the situation at Foula, situated approximately 1km inland. Similarly, Maxson and Bernstein (1982) found that blue-eyed shags only regurgitated fish when attacked by South Polar skuas if their most effective means of escape (ie landing on the water) was precluded by the presence of ice floes. In view of these differences, it is preferable that when the success rates of two species are compared, they should be studied at the same location. When the success rates of skuas and "gulls" recorded solely at Foula were compared, in all but one comparison, the success rates of the skuas were significantly higher than those achieved by the "gulls". Even in the case of the non-significant result, the Arctic skuas were more than twice as successful as the "gulls". Although not statistically significant such a difference in success rate must surely be of biological significance to the species concerned. These results agree with those of two other studies, (Arnason and Grant 1978, Forssgren 1981), in which the success rates of skuas were found to be higher than those of gulls, chasing the same species, at the same site.

These three results support the prediction that, when compared directly, the success rates of "specialist" kleptoparasites should be higher than those of "oppportunist" kleptoparasites.

5) Host selection patterns of skuas in relation to success rates

Optimal foraging theory predicts that animals should optimise their feeding activities in order to either maximise their net rate of energy intake (energy maximisers) or to minimise the amount of time needed to obtain a fixed amount of energy (time minimisers) (Schoener 1971). Foraging kleptoparasites usually have a variety of potential host species to attack which differ in their ability to escape, tendency to release their food and in the size of the food items which they carry. Several studies have shown that the foraging behaviour of kleptoparasites is consistent with the predictions of optimal foraging theory in that they preferentially select hosts; against which they have the highest chance of success (Furness 1978a, Taylor 1979), which carry the largest prey items (Hatch 1975, Arnason and Grant 1978) and which yield the greatest net reward (Furness 1981a, Thompson 1986). Kleptoparasites have also been found to use the most profitable attack strategies (Hudson 1985, Thompson 1986). A simple model to examine the host selection pattern of skuas in terms of the net energy per unit time chasing takes the form,

$$\text{Net } E = \frac{(W.P)-C,}{T} \qquad (2.1)$$

where Net E is the net energy gain per unit time from an attack, W is

the gross energy content of the food being attacked, P is the probability of the attack being successful, C is the average energetic cost of the attack and T is the attack duration. According to classical optimal foraging theory (Krebs et al. 1983) animals should take unprofitable items when encounter rate with profitable items is low, should increase their selectivity for the most profitable items as the encounter rate with such items increases and should ignore unprofitable prey items, regardless of encounter rate, when encounter rate with profitable items is high.

On the basis of information which was collected in 1986 and 1987, and that is presented in Table 2.36, the net energy gain per unit time spent chasing the three main host species was calculated for Arctic skuas and great skuas in 1986 and 1987 (Table 2.36). These figures must be treated with caution because; values for energy content of fish were determined from a small sample of fish collected only in 1987, the number of fish secured per successful chase was recorded only in 1987, and the values for the average energetic cost of attacks were based on observations of the proportions of attacks which involved flapping flight that were made only in 1986. Bearing these factors in mind, the results indicate that puffins were the most profitable species for great skuas to chase in both years because, they secured more fish per successful chase when chasing puffins than when chasing guillemots and also because they had a much higher success rate when chasing puffins. Guillemots were the most profitable species for Arctic skuas to chase because of the large sizes of fish

which guillemots carried. Given these findings, great skuas might have been expected to preferentially chase puffins and Arctic skuas to preferentially chase guillemots. In 1986 and 1987, great skuas did indeed chase puffins more than expected on the basis of their availability. The fact that great skuas chased all three species of auk and not just the most profitable one (ie puffins) implies that the encounter rate with profitable prey was too low to allow them to specialise completely and ignore the other two species of victim (Emlen 1968, Schoener 1971, Krebs et al. 1983, Pyke 1984). However, contrary to expectations Arctic skuas chased guillemots no more than expected on the basis of their availability in either year and, like great skuas, selectively chased puffins, which in their case were not the most profitable victims. This should never occur in an optimal diet (Pyke 1984). However, these patterns of host selection were derived from observations made between June and August during which time the availability of the three species of auk changed dramatically. On certain days the number of guillemots arriving with fish outnumbered the number of fish-carrying puffins, but by the end of July guillemots had almost all left the island, and only puffins were available to be chased. This fact, in conjunction with the tendency of Arctic skuas to chase a higher proportion of arriving birds late in the season (Grant 1971), may explain why Arctic skuas chased puffins preferentially over the course of the whole season. Hence although the host preference patterns of Arctic skuas do not

agree with the predictions of optimal foraging theory, the results do not indicate whether Arctic skuas were foraging optimally on a daily basis.

6) Changes in the success rates of skuas

Comparison of the success rates of Arctic skuas between years revealed that, against certain species of host there were significant differences. Arctic skuas were more successful against Arctic terns in 1975-76 and 1979 than in 1978 and 1980. Furness (1980) could suggest no reason for the differences between years in the success rates of chases of Arctic terns by Arctic skuas. However, it seems fairly clear that success rate depends on the breeding success of the terns since the success rates recorded in 1975-76 and 1979 (which were all years of good tern breeding success, with a production of 0.67, 0.71 and 0.68 chicks per pair respectively (Furness 1987c)), were higher than in 1978 and 1980 (which were both years of poor tern breeding success, with production of 0.08 and 0.50 chicks per pair respectively (Furness 1987c)).

In 1988, the shortage of sandeels around Shetland produced a much more widespread and pronounced reduction in breeding success of seabirds than in 1986 or 1987. Not all species were affected with equal severity, for while guillemots and gannets were essentially unaffected, puffins on Foula had an almost complete breeding failure. No data on the breeding success of puffins on Foula were recorded in 1986 or 1987, but given that both species of skua were showing warning signs of the disaster to come in 1988, (see chapter 4), it is likely

that puffins were as well. It is, therefore, interesting that the only species against which the success rates of skuas were significantly lower in the last two years than in the past, is the puffin. Given these findings, it seems reasonable to conclude that the success rates of skuas against a given species of host depends heavily on the breeding success of that species. One possible explanation for this is that during a food shortage, victims are less willing to give up their catch to an attacking skua (Furness 1987a,b). Support for this idea comes from the data of Andersson (1976). Andersson found that in 88 chases of puffins by Arctic skuas, only in 4 chases (4.5%) did the skua make contact with the victim. Data from 1986 reveals that in chases of puffins, contact occurred between Arctic skuas and their victims in 25.7% of 918 chases. Since the food-releasing behaviour of hosts is assumed to be a strategy to minimise the likelihood of injury due to contact, or of predation (Grant 1971, Brockman and Barnard 1979), it appears that puffins are now less willing to release their fish, even at the risk of injury to themselves. The puffins' cost-benefit balance between risking injury and feeding their chicks as often as possible seems to have shifted towards the latter under the conditions of reduced food availability in the last few years.

Furness (1980) suggested that "the utilisation of available hosts by Arctic skuas at Foula depends largely on the relationship between Arctic tern breeding numbers and success and the sizes of the sandeels carried by puffins relative to the sizes of those carried by

Arctic terns". She further suggested that "the breeding numbers and success of puffins presumably would be equally important, but do not seem to have been as variable".

In recent years there has been a marked reduction in the populations and breeding success of many species of seabird in Shetland, (Furness 1987c, see chapter 4). Arctic terns have been the most severely affected species and have reared no young on Foula since 1984 where their population has declined from 6000 pairs in 1975 to a mere 300 pairs in 1987. Given these changes ,the finding that the success rates of chases of puffins have decreased significantly in recent years and that the success of chases of Arctic terns by Arctic skuas seems to vary with the breeding success of the former, it might be expected that the pattern of host selection by skuas will have changed.

7) Changes in the host selection patterns of skuas

Since Arctic tern breeding success was similar in 1975-76 and 1979, the fact that the host selection pattern differed significantly between these years cannot be explained by changes in the breeding success of the Arctic terns. Between these two periods, the breeding population of Arctic terns on Foula decreased from 6,000 pairs to 4,400 pairs, a reduction of 26.7% (Furness 1987c). Thus as suggested by Furness (1980) the number of breeding terns available influenced the host selection pattern of Arctic skuas. A similar trend is apparent in the comparison of host selection patterns of Arctic skuas

between years of poor Arctic tern breeding success (ie 1978 and 1987). Again, since the breeding success of Arctic terns was similar in these two years, the most likely explanation for this difference is that the population of Arctic terns on Foula was 88.5% lower in 1987 than in 1978 (Furness 1987c). Since Arctic skuas normally switch to chasing puffins when Arctic terns are either unavailable and/or are having a poor breeding season (Arnason and Grant 1978, Furness 1980) the fact that Arctic skuas chased razorbills more preferentially in 1987 than in 1978 rather than puffins, must indicate that puffins were not as good a "second choice" as is usually the case. Given the breeding failure of puffins in 1988, this finding could reflect the likelihood that in 1987 puffins were already suffering a reduction in breeding success and hence not "worth concentrating on" any more than usual.

Like Arctic skuas, great skuas have altered their host selection patterns since 1975. Although the major changes in their case involved altered preferences for gannets, kittiwakes and guillemots, they too chased puffins less often in 1987 than in 1975-76. On the whole, both species of skua seem to alter their host selection patterns depending on the availability and breeding success of their host species, as has been suggested to be true of Arctic skuas (Furness 1980).

8) Differences in the host preferences of Arctic skuas and great skuas

Furness (1978a) found that on Foula, great skuas and Arctic skuas differed in their host selection patterns. This was also true in the

present study. However, in this case the result can be explained by the fact that the chases by the two species of skua were recorded at different locations on the island between which the host availability differed significantly in exactly the same manner as the host selection patterns. Thus the spatial segregation of Arctic skuas and great skuas seems sufficient to explain their different host preferences. It is unlikely that the different success rates achieved by the two species of skuas against puffins, guillemots and razorbills affects their patterns of host selection since chases by single great skuas were almost always significantly more successful than chases by single Arctic skuas. As suggested by Furness (1978a), differential success rates between the two species of skua can probably explain why great skuas and Arctic skuas both chase some species which the other does not. Furness (1978a) discussed the extent of niche overlap between Arctic skuas and great skuas on Foula. He concluded that the differences in the preferred victim of the two species of skua and the tendency for each skua species to concentrate its kleptoparasitic foraging in areas where their preferred victims are most numerous minimised the competition between the two species. In view of the dramatic decline in the breeding population of one of the Arctic skuas' most preferred victims (ie Arctic terns) on Foula, it is likely that competition between great skuas and Arctic skuas has increased since the mid-1970s.

9) Methods of forcing victims to release fish, and efficiency in securing dropped fish

As expected, light and melanic Arctic skuas differed very little in how they induced their victims to part with their fish, or in their ability to secure fish that were dropped. However, although only significant in one instance, in those chases which resulted in the attacker securing fish dropped by the victim, light phase Arctic skuas always secured the fish before they hit the sea more often than melanic phase birds. Since the ability of Arctic skuas to secure fish in the air depends on the height from which the fish are dropped, (Grant 1971, Arnason and Grant 1978), these results probably reflect the fact that light phase birds tended to chase higher-flying victims than melanic phase birds. The fact that great skuas tended to chase higher-flying victims than Arctic skuas and yet did not catch a higher proportion of fish in the air, indicates that great skuas are not as agile and adept at twisting and turning to catch fish in mid-air as are Arctic skuas. This suggestion is supported by the finding that in all comparisons, Arctic skuas induced their victims to release their fish much more often than great skuas, by approaching the victims very closely and stealing the fish directly from their bills Such manoeuvres require great agility on the part of the skua.

Perhaps the most surprising difference between Arctic skuas and great skuas was that in all comparisons, Arctic skuas secured a significantly lower proportion of fish that were dropped by victims which were still flying, than did great skuas. This was all the more

surprising because the two species did not differ either in their ability to secure fish in mid-air, or fish which, having been dropped and missed in the air, landed on the sea-surface. The reason for these anomalous findings lies in the topography of the two sites where chases were recorded. Heddlicliff, where practically all the chases by Arctic skuas were recorded is a low, gently-sloping cliff with a considerable area of boulder-scree at its foot. At Kittiwakes' Haa, where practically all the chases by great skuas were recorded, the cliff is sheer and has no tallus at its base. The result of this difference was that while very few of the fish dropped by the victims of great skuas landed anywhere other than in the sea, over 30% of those dropped by the victims of Arctic skuas landed on the rocks at the foot of the cliff. Since the ability of Arctic skuas, (and presumably of great skuas), to secure fish which landed on the rocks was much less than their ability to secure fish from the sea-surface, the poorer success rate of Arctic skuas in securing fish dropped by their victims, in comparison to great skuas, can be explained.

The inability of skuas to secure fish which landed among the boulders at the foot of Heddlicliff was very similar to the findings of Grant (1971) and Arnason and Grant (1978). They found that Arctic skuas chasing puffins, most often secured fish in the air while fish that fell to the ground were more often taken by gulls. Arnason and Grant (1978) also found that the chances of an Arctic skua securing a fish which had landed on the ground were directly related to the

structure and density of the vegetation into which the fish fell. The longer and denser the vegetation, the less likely the skuas were to be successful. Gulls on the other hand found no problem in securing fish from such thick vegetation. The reason for this difference between gulls and skuas was that while the former picked up fish as they walked among the vegetation, skuas attempted to secure fish that were on the ground by hovering over the surface without touching the ground. Arnason and Grant (1978) pointed out that the skuas needed free space to do this and hence that dense vegetation impeded them. Among the boulders at the foot of Heddlicliff, lack of free airspace was also likely to have been the main reason why skuas hardly ever secured fish that landed there while gulls acting as gleaners were quite successful in this habitat.

10) Factors affecting the outcome of chases

Furness (1978a) carried out a stepwise multiple regression to examine the factors which determine whether or not a chase is successful. The results of the stepwise discriminant analyses, in conjunction with the chi-square tests used in the present study are very similar to those of Furness (1978a). In all cases, chases were more likely to be successful if the speed of reaction of the victim was slow, and if the attacker managed to get within one metre of the victim and make contact with it (the latter two variables not being statistically significant when chases of puffins by great skuas were considered). These three variables are all clearly related to one another, since if the victim took evasive action early enough, and

flew away from the attacker, then the skua was much less likely to get close to the victim and hence less likely to contact it. The effect of physical contact between victims and attackers on the likelihood of the former releasing their fish is a very interesting subject, but one which few authors have studied. In agreement with the results of the present study, Andersson (1976) and Maxson and Bernstein (1982), found that the likelihood of victims regurgitating fish, increased if the their pursuer managed to make physical contact with them. These results must arise because victims which have been caught by their attackers, and hence in grave danger of being injured or killed, are more willing to give up their food than those which are in less immediate danger (Grant 1971, Brockman and Barnard 1979).

When chased, auks almost invariably descended to the sea surface as rapidly as possible, unless they were low over the water to begin with. When skuas attacked from above, particularly by means of a stoop on closed wings, (as was fairly typical of great skuas), the attackers were travelling extremely rapidly in the direction in which the auks almost always tried to escape. In this situation, the chances of an auk keeping a safe distance between itself and an attacker until it reaches the sea-surface are probably greater, the less height it itself has to descend to the sea. Thus auks which were high above the sea when attacked, may have "realised" that their chances of reaching the safety of the sea surface before being caught were small, and released their food more readily than ones which were low over the

water, and hence nearer to safety, to begin with.

Support for this idea comes from the difference in the importance of the height of the victim on the likelihood of success between the two species of skua and the differences in how they usually attack their victims. Great skuas initiated a significantly higher proportion of their attacks with rapid descending swoops from above and behind their victims than did Arctic skuas. This is the sort of attack in which the likelihood of the victim reaching the sea safely is most likely to depend upon its height above the sea at the start of the chase. Hence, it is not surprising that the effect of the victims' initial height on the probability of success was more pronounced for great skuas than for Arctic skuas.

Andersson (1976) found that when chased by Arctic skuas, puffins were much more likely to drop their fish when chased towards the cliff than when they descended away from the cliff to the sea surface. This was also the case in the present study. Maxson and Bernstein (1982) found a similar result during a study of interactions between South Polar skuas and blue-eyed shags, although the underlying reason was quite different. The results of Grant (1971) and Arnason and Grant (1978) indicate that when chased by Arctic skuas, puffins were more likely to drop their fish when chased away from the cliff. These latter results are somewhat surprising given that puffins which were being chased away from the cliff were getting progressively nearer the sea and safety. Perhaps these results reflect the atypical inland situation of the breeding cliff at which these studies were carried

out. At Shetland colonies, puffins which were chased away from a cliff had effectively no distance to cover before reaching the sea, whereas at the Iceland colony they had to fly approximately 1km before reaching safety. Thus the contrary results of the studies in Shetland and Iceland may simply reflect the possibility that, relative to the chances of escape when approaching the cliff, the likelihood of escape when being chased away from a cliff was far higher in Shetland than in Iceland.

Discriminant analysis indicated that chases by Arctic skuas were more likely to be successful if they were initiated with descending flight. Chi-square analyses indicated that in the larger sample the significance of this variable was fairly marginal, particularly when considering chases of all species together. However, it is interesting that the likelihood of success for Arctic skuas was lowest when they initiated chases with level flight from the same height as the victim, (Table 2.35). This agrees well with the fact that the likelihood of the victim being slow to react was lowest when attacked from the same height by either light or melanic Arctic skuas, (Table 2.34). The same would seem to be true for great skuas, although the samples of chases which were initiated from anywhere other than above are small. Perhaps this indicates that auks are able to see objects which are at the same height as themselves more readily than objects which are above or below them.

The chi-square analyses also indicated that, chases by Arctic skuas, unlike those by great skuas, were significantly more likely to be successful, the longer they continued and if the skua made any rapid turns. Furness (1978a) found that chase duration was an important determinant of Arctic skua chase success, particularly in chases of Arctic terns and kittiwakes, and also of great skua chases of "gulls". He concluded that persistence was not a quality peculiar to Arctic skuas but was a necessary attribute for any skua which attempts to rob terns or gulls. However, Furness (1978a) did find that when chasing puffins, Arctic skuas were more likely to be successful the longer the chase continued while great skuas were not. This is exactly the same result as found in the present study.

Furness (1978a) also found that chases of puffins by Arctic skuas were likely to last longer if the victim was slow to react and high above the sea. Since these two variables were found, either by the discriminant analyses or chi-square analyses, to affect the likelihood of success, it is clear why chase duration influenced the success of Arctic skuas. Similarly the apparent influence of the use of rapid changes of direction by Arctic skuas on the likelihood of success can be explained by the fact that rapid changes of direction by Arctic skuas usually occurred when the victim was slow to react. The apparent influence of the use of flapping flight on the likelihood of success of chases of puffins by Arctic skuas probably reflects the fact that the longer a chase lasted, the more likely it was that the skua would have to begin flapping to keep up with or close in on the victim.

Contrary to the results of Arnason and Grant (1978) chases by Arctic skuas were less likely to be successful if the victim was far from the cliff when the chase began. Again this may reflect the different topography of the the two study sites. At the Iceland colony, puffins approaching the cliff, but still a long way from it when the chase began, were more likely to release their fish than those which were closer to the cliff, perhaps because they had further to go to reach the safety of their burrows, with no possibility of escaping into the sea. At Shetland, those victims that were far from the cliff when the chase began were always over the water and hence could easily escape to the sea. Those that were near to the cliff may have been over the tallus when the chase began, and although close to their burrows, may have had no immediate escape route, and hence were more willing to release their fish. This would be particularly likely if the skuas prevented the puffins from landing at their burrows by flying between them and the cliff, as was observed by Arnason and Grant (1978).

11) Attack strategies of Arctic skuas and great skuas

Kleptoparasites employ a wide variety of attack strategies ranging from the collision tactics of lesser sheathbills (Chionis minor) (Burger 1981) and the ground-based attacks of gulls (Hulsman 1976, Fuchs 1977, Burger and Gochfeld 1981, Greig et al. 1983, Hudson 1985, Rice 1987) to the typical high speed aerial pursuits of gulls and terns (Hatch 1970, 1975, Hopkins and Wiley 1972, Dunn 1973, Hulsman 1976, Burger and Gochfeld 1981, Thompson 1986) and skuas (Grant 1971,

Andersson 1976, Arnason 1978, Arnason and Grant 1978, Furness 1978a, 1981a, Taylor 1979, Furness and Furness 1980, Maxson and Bernstein 1982, Birt and Cairns 1987). Even within the category of aerial attacks, the strategies employed are varied and Furness (1978a) noted that the Arctic skua and the great skua differ in the methods of aerial attack which they employ. No study has attempted to quantify differences in attack strategies between species of kleptoparasite. The most fundamental differences which were found in this study were that great skuas began a significantly higher proportion of their chases than Arctic skuas, with rapid descending stoops from above and behind their victims without using flapping flight. It is almost certain that attacks which were initiated in this way, and which did not involve flapping flight, required considerably less energy to be expended by the attackers than any other kind of chase. Perhaps great skuas' more frequent use of this type of attack compared to Arctic skuas reflects the fact that the high speed flapping chases typical of Arctic skuas are considerably more energetically expensive to great skuas than they are to Arctic skuas (relative to basal metabolic rate, see chapter 3), as a consequence of the morphological differences between the two species (see chapter 6). The fact that great skuas selected high-flying victims significantly more often than Arctic skuas might indicate that great skuas were attempting to maximise their chances of success since chases by great skuas were more likely to be successful if the victim was high above the water when the chase began. However, once again the spatial segregation of the two species

of skua and the different topography of the two sites offers an alternative explanation.

At Heddlicliff, auks nested at all levels of the cliff, but since the cliff is only 40m high, all nests were below this height. At Kittiwakes' Haa, the cliff is about 200m high, and many auks had their breeding ledges or burrows higher than 40m above sea-level. Since auks typically approach their ledges or burrows with either level flight, (Furness 1978a), or in a shallow dive, (Pennycuick 1987a), they typically begin their approach at either the same height or slightly above their landing target. This behaviour of auks, together with the difference in the heights of their breeding sites at the two observation points may explain why victims of great skuas tended to be higher when chases were initiated than those of Arctic skuas.

Since Arctic skuas appear to hunt close to their nesting territories (Furness and Furness 1980) the spatial segregation of the two species of skua at the cliffs may simply reflect the breeding distribution of Arctic skuas on the island. However, great skuas nest all over the island and there would seem to be no obvious reason why they should be almost absent at the cliffs where Arctic skuas were abundant. Furness (1978a) suggested that the lower success rates of great skuas chasing puffins at Hermaness in comparison with their success on Foula was due to the relatively low cliff height at the former colony. Perhaps the tendency of great skuas to chase at the higher cliffs on Foula reflects the fact that with the attack strategy which they typically

employ, the height of the available hosts is very important in determining the profitability of the feeding strategy. Hunting at low cliffs may require a different attack strategy, perhaps more akin to the high speed flapping pursuits used by Arctic skuas. It is certain that the cost of kleptoparasitic foraging to great skuas would be greater if they had to chase in this way all the time. Hence, great skuas may concentrate their efforts where it is possible to successfully carry out energetically inexpensive stooping attacks (ie at high cliffs). Perhaps Arctic skuas would fare better if they carried out more chases at the high cliffs where great skuas were most active. However, in this situation the Arctic skuas would have to hunt alongside relatively high numbers of great skuas and as Furness (1978a) pointed out, both species may suffer a reduced availability of their preferred victims as a result of the presence of the other skua species. This would obviously be a more serious problem for the more specialised Arctic skuas than for great skuas which feed largely by other means.

Another difference in the attack strategies of great skuas and Arctic skuas was that chases by the former were less likely to involve pursuit towards or parallel to the cliff, and more likely to involve pursuit away from the cliff, particularly when only chases of puffins were considered. Quite why this should be the case is unclear.

It is also unclear why the speed of reaction of victims was generally faster to great skuas than to Arctic skuas. Perhaps this simply indicates that the larger the attacker, the easier it was to

detect. For reasons which have been outlined above, this result explains why great skuas got close to their victims, and made contact with them, much less frequently than Arctic skuas. Skuas tend to give up chases more quickly if the victim reacts rapidly to them, (Taylor 1979, pers obs). Thus the difference in the victim's speed of reaction to the two species of skua, explains why attacks by great skuas generally were of shorter duration than those by Arctic skuas. Arctic skuas tended to make rapid turns during a chase when the speed of reaction of the victim was slow and when they approached from the side or in front of the victim (pers. obs.). In these cases, skuas had to turn rapidly in order to change their direction of flight and follow the escaping victim. Since the speed of reaction of victims to great skuas tended to be faster than to Arctic skuas, and great skuas began far fewer chases from the side of, or in front of their victims, it is not surprising that great skuas employed rapid changes in direction less often than Arctic skuas.

As found by Furness (1978a) great skuas elicited diving in a higher proportion of their chases than Arctic skuas. Given that great skuas are much more of a threat to their victims than Arctic skuas, in terms of their tendency to prey on auks, this result is as expected.

In conclusion, the results of this study neither refute nor prove the validity of the apostatic selection hypothesis, although the changes in the success rates of light and melanic phase Arctic skuas which have accompanied the changes in their relative abundance are, on

the whole, as the theory predicts. The formation of group attacks by skuas appears to be a purely selfish behaviour on the part of the joiners. The greater success rates of skuas in comparison with those of gulls, chasing the same species at the same location, supports the classification of these two families as "specialist" and "opportunist" kleptoparasites respectively. The host selection patterns of skuas seem to depend on the numbers of different host species that are available to them and on the profitability of chasing each species, which itself may depend on the breeding success of the hosts. With their greater agility, Arctic skuas steal fish directly from the bills of their victims significantly more often than great skuas, although great skuas are more successful than Arctic skuas at inducing their victims to release their fish and at securing dropped fish. This latter result is a consequence of spatial segregation of the two species of skua which itself may be a consequence of the breeding distribution of Arctic skuas on the island, or a lack of willingness on the part of Arctic skuas to hunt where there are large numbers of great skuas, or the lower success rate and hence profitability of this feeding strategy to great skuas when hunting at low cliffs. This latter possibility could arise because the great skuas preferred attack strategy is less successful at low cliffs where alternative, but more energetically expensive strategies are appropriate. Great skuas may not be able to utilise such strategies as profitably as Arctic skuas because of fundamental differences in their morphology and flight capabilities.

Chapter 3

Energetic profitability of kleptoparasitism.

Introduction

Arctic skuas (Stercorarius parasiticus) which breed in Shetland feed almost entirely by kleptoparasitism (Furness 1980, Furness 1987a). Thus the daily energetic reward from kleptoparasitic foraging to a pair of breeding Arctic skuas would be expected to approximately equal the amount of energy required each day to sustain both themselves and their chicks.

Great skuas (Catharacta skua) which breed in Shetland feed largely by catching fish for themselves or by scavenging discarded whitefish from behind fishing boats (Furness and Hislop 1981, Hudson 1986, Furness 1987a, Hudson and Furness 1988). Contrary to popular belief, great skuas in Shetland obtain very little of their food kleptoparasitically (Furness and Hislop 1981, Furness 1987a). Nonetheless, if kleptoparasitism is considered to be a feeding strategy (Brockman and Barnard 1979) which is exhibited either occasionally by all individual great skuas or one which is used all of the time by a few individuals, then its profitability in terms of long term reproductive success must be as high as that of the other feeding strategies employed by great skuas. If this were not the case then selection would occur against those individuals which either use this feeding technique all the time or those that resort to feeding in this way too often (Brockman and Barnard 1979), and the behaviour would disappear. Since adult survival of great skuas is very high (Furness

1978b) and great skuas do breed successfully in Shetland, the main feeding techniques employed by the species must yield sufficient energy to meet the needs of each breeding pair and their chicks. Thus for kleptoparasitism to persist as a feeding behaviour in the population, the energetic reward from feeding in this way should also approximately equal the requirements of adults and their chicks.

Although individual great skuas do specialise in particular feeding techniques (Bayes et al. 1964, Furness 1987a), it is unlikely that the kleptoparasitic chases observed at Foula were carried out by only a few pairs of birds feeding in this way all the time. It is more likely that the chases observed were the result of the activities of all the birds on the island utilising this feeding technique occasionally in preference to other methods of feeding. Thus, calculation of the daily energy balance of specific pairs of great skuas, on the assumption that the adults were feeding entirely by kleptoparasitism, can only serve to indicate whether it is theoretically possible for great skuas to breed successfully when feeding entirely in this way since it is very unlikely that the pairs in question were actually doing so.

Methods

1) Collection of time budget data

In the late spring of 1987, three neighbouring pairs of great skuas, (pairs A, B and C) and three pairs of Arctic skuas, (pairs X, Y and Z) which were holding territories adjacent to one another at a different location on the island, were selected for detailed time-budget

analyses. The individual members of each pair could readily be distinguished either by phase, in the case of the Arctic skuas, or by distinctive plumage markings. The sex of each bird in each pair was determined by observation of copulatory position.

Pair A reared two young to fledging and then one until the end of the season following the predation of one of their chicks. Pair B layed two eggs of which only one hatched. They reared this chick until the end of the season. Pair C layed one egg which failed to hatch. A neighbouring pair of great skuas (pair D) which were at a similar stage was selected as a replacement. Unfortunately the chicks of this pair died young and another pair (pair E) was selected to replace them. Pairs D and E were at a similar stage in the chick-rearing process. In order to cover the whole chick-rearing period, observations made on the latter pair, after the death of the chicks of the former pair, were combined with those made initially on pair D. Pair E reared two chicks until the end of the season. Pairs X, Y and Z each layed two eggs all of which hatched. However, pair X reared three chicks until fledging since one of the chicks of pair Y wandered into their territory at an early age. One of these chicks was killed by great skuas after it had fledged and the other two "disappeared", possibly having left the island. Pair Y reared only one chick to fledging and this also "disappeared" at fledging age. Pair Z reared both their chicks until fledging but both fledglings were subsequently killed by great skuas. All observations made after a pair's breeding

attempt was believed to have failed (on the grounds of the "disappearance" of the chicks or the discovery of dead chicks) were excluded from the analyses.

Observations were made from two hides, one overlooking the territories of the pairs of great skuas under study as well as those of their neighbours and the other overlooking the territories of the three pairs of Arctic skuas and two other pairs breeding nearby.

Watches lasted for six hours unless curtailed by poor light at nightfall. Successive watches on each species covered a different quarter of the day. Sufficient watches were carried out to obtain records for at least two 24 hour periods during each stage of the breeding cycle (ie pre-laying, incubation and chick-rearing). Between the 25th of April and the 23rd of August a total of 1566 bird hours was recorded for great skuas. Between the 12th of May and the 31st of July a total of 1038 bird hours was recorded for Arctic skuas.

For two reasons, only observations made after chick-hatching are considered in estimating whether the energetic reward from kleptoparasitism was sufficient to meet the requirements of each pair of skuas. Firstly, the chick-rearing period of the breeding cycle is likely to be the most costly to a pair of skuas (due to the fact that they have ckicks to feed and to the increased amount of energetically expensive foraging which they do at this time (see chapter 4)), and hence the period when the optimisation of foraging behaviour is probably most critical (Kushlan 1978). Secondly, kleptoparasitic chases occurred only infrequently until the end of the second week in

June. By this time, all the study pairs of skuas were at least half-way through the incubation period and the great skuas' eggs were about to hatch. Thus it was not possible to determine the profitability of feeding kleptoparasitically during the weeks immediately preceding egg-laying or during the incubation period.

During each observation period the behaviour of the birds was studied by instantaneous sampling (Altmann 1974). Spot observations were made on successive pairs at two minute intervals so that the behaviour of both members of each pair was recorded simultaneously once every six minutes.

The behaviour of great skuas and Arctic skuas during the chick-rearing period was classified into several distinct categories as follows; resting, comfort behaviour (ie preening, scratching, stretching, bill-cleaning, pellet ejection, drinking, bathing), pair displays , feeding self or chicks, walking about the territory, flying across the territory to change position, agonistic display (ie alarm call, long call, bend, oblique, wing raising), running pursuit of intruder, flying pursuit of intruder, territorial display flight, fighting, or absent.

The percentage of time spent in each of these activities by each bird during the chick-rearing period was calculated for every hour of the day by pooling all the data from watches made during that period. The daily time budget on an average day during the chick-rearing period was determined for each bird by calculating the mean of the

percentages of time spent in each activity during each hour.

2) Calculation of energy requirements

These time budgets were converted to energy budgets by using literature-derived empirical estimates of the energetic cost of each activity expressed as multiples of basal metabolic rate (BMR). This technique has been utilised by several authors (Arnason and Grant 1978, Furness 1978c, Tarboton 1978, Holmes et al. 1979, Burger 1981, Mugaas and King 1981, Rudolph 1982, Finch 1984, Gaston 1985, Birt and Cairns 1987). Unless otherwise stated, the estimates of the costs of various activities which were used by Burger (1981), in a study of the energy needs of lesser sheathbills (Chionis minor), were used in this study.

Resting was estimated to cost 1.5 times BMR. Comfort behaviour was estimated to cost 2 times BMR. Unlike lesser sheathbills, agonistic displays (equivalent to the antipredator aggression category of Burger (1981)), by skuas involve very little if any walking let alone running. Thus a value of 2 times BMR was selected instead of 4 times BMR suggested by Burger (1981). Feeding of chicks, especially large ones, and foraging by adults for themselves while on the territory usually involved a good deal of walking and sometimes running. This was also true of pair displays. Each of these activities, as well as walking about the territory, was estimated to cost 3 times BMR. This is lower than the value of 4 times BMR suggested by Burger (1981) for activities which involved walking or running. Burger (1981) proposed this value on the basis of the data of Holmes et al. (1979) who assumed

that hopping in passerines costs 5 times BMR. This value was considered to be too high by Williams and Nagy (1984). Running across the territory in pursuit of an intruder was estimated to cost 4 times BMR.

Powered flapping flight is the most energetically expensive activity which birds undertake (Berger and Hart 1974). Thus any error in the assignment of an energetic equivalent to flight will have very pronounced effects on total energy requirements which are calculated. This is particularly true if flight occupies a major proportion of the birds' time. Bryant et al. (1984) concluded that the most likely source of error in their calculation of the daily energy expenditures of Pacific swallows (Hirundo tahitica) and blue-throated bee-eaters (Merops viridis), both of which spent a large proportion of their time in flight, was indeed their estimates of in-flight metabolism. Thus, it was decided to give careful consideration to the estimate of the cost of flight to be used in this study.

On the basis of empirical data on the energy expenditure of birds in flight, measured by a variety of methods including weight loss over long flights and the consumption of O_2 and production of CO_2 by birds flying in wind tunnels, Berger and Hart (1974) and Kendeigh et al. (1977) derived allometric equations for the cost of flight based solely on body mass. However, as pointed out by Masman and Klaassen (1987), the energy expenditure during flight varies among birds of the same mass due to differences in the aerodynamic and behavioural

properties of the species (Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984, Rayner 1979). Thus calculation of the flight costs of skuas on the basis of their mass alone was not considered satisfactory.

The idea that flight is equally hard work for all species and that its cost can be expressed as a fixed multiple of basal or standard metabolic rate was first proposed by Raveling and LeFebvre (1967). They suggested that flight requires energy expenditure at the rate of 12 times standard metabolic rate (SMR). Since then several studies of the energetic costs of flight determined either by oxygen consumption of birds flying in wind tunnels (Berger et al. 1970, Tucker 1972, Bernstein et al. 1973), or by the doubly labelled water technique (Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984, Adams et al. 1986, Costa and Prince 1987, Obst et al.1987, see also Masman and Klaassen 1987) have indicated that as suggested by Nisbet (1967), the hypothesis of Raveling and LeFebvre (1967) is not correct. Pennycuick (1982) pointed out that according to aerodynamic theory, the power required for flapping flight at any speed scales more rapidly with mass than does metabolic power. Thus the ratio of mechanical to metabolic components is larger in large birds than in small ones. Therefore, as stated by Pennycuick (1982), it is not valid to assume that the total power required to fly is a constant multiple of the metabolic power in birds of different mass. The ratio of metabolic rate in flight to basal metabolic rate is greater in large birds than in smaller ones (Pennycuick 1975). For these reasons it was decided

not to select any commonly used multiple of BMR as an estimate of the cost of skuas' flight.

Instead, it was decided to utilise the morphological measurements made on corpses of great skuas and Arctic skuas (see chapter 6), and to calculate the cost of powered flight according to the aerodynamic theory developed by Pennycuick (1968b, 1969, 1975).

In order to calculate the total power required to fly, the basal metabolic rate of the bird must be determined initially since this is one component of the total power required (Pennycuick 1975). Basal metabolic rate can be calculated from allometric equations, based on empirical measurements, such as those of Lasiewski and Dawson (1967), Aschoff and Pohl (1970), Kendeigh et al.(1977). However, data in Ellis (1984) indicate that in many species of seabird, measured values of BMR differ markedly from values predicted from such allometric equations. Ricklefs and Matthew (1983) found that the rate of oxygen consumption by South Polar skuas (Catharacta maccormicki) was 1.96 times as high as that predicted by the equations of Lasiewski and Dawson (1967). The SMR of the South Polar skuas, which they measured at ambient temperatures of between 2°C and 9°C, was 1.301 O2/kg/hr which, is equivalent to 29.18kJ/hr. From equation 5.15 of Kendeigh et al.(1977) the SMR of these birds at 0°C was estimated to be 25.22kJ/hr while from equation 5.5 of Kendeigh et al. (1977) their BMR was calculated to be 15.92kJ/hr. The critical temperature at which SMR=BMR was estimated to be 13.22°C (Kendeigh et al. 1977 eqn 5.12). This value

is almost certainly too high, given the adaptations which skuas exhibit for thermal insulation (see discussion), but is the best estimate currently available. By interpolation (Wiens and Innes 1974) the SMR of the South Polar skuas at 5.5°C (the mean of 2°C and 9°C) was estimated to be 21.35kJ/hr. Thus the measured SMR was 1.367 times higher than the value predicted by the equations of Kendeigh et al. (1977). This implies that the equations of Kendeigh et al.(1977) give a better approximation of the measured metabolic rate than the equation of Lasiewski and Dawson (1967). When the BMRs of great skuas and Arctic skuas were estimated from the equations of Kendeigh et al. (1977) the resulting figures were multiplied by 1.367, on the assumption that this elevated metabolic rate of South Polar skuas is typical of all skuas. Recent work on Arctic skuas (Furness, Anderson and Bryant in prep.) seems to indicate that this is indeed the case.

The basal metabolic rate (and the cost of powered flapping flight) were estimated separately for each sex of the two species of skua since both species exhibit marked reversed sexual size dimorphism (Furness 1987a). Arctic skuas are the most sexually dimorphic species of skua; females weigh on average 16.5% more than males (Furness 1987a). This fact was not taken into account by Furness (1980). The morphological parameters which were used in the calculation of the cost of flight are given in Table 3.1.

Initially the minimum power speed (V^{mp}), the absolute minimum power required to fly (P^{am}), and the maximum range speed (V^{mr}) were calculated from equations 5.13, 5.14 and 5.15 (see chapter 5). The

metabolic power ratio (X2) was then calculated from equation 5.21. The total power required to fly at V^{mp} and V^{mr} was calculated from equation 25 of Pennycuick (1975). These values, which were expressed in Watts were converted to kJ/hr and divided by the muscular efficiency factor of 0.23 (Pennycuick 1975) to yield the energy consumption. These values were then divided by the pre-determined values for BMR and expressed as multiples thereof.

The cost of gliding flight was taken to be 3.1 times BMR for both sexes of both species of skua (Ellis 1984). The cost of flying across the territory and of territorial display flights was assumed to be equivalent of flight at V^{mr}. Kendeigh et al. (1977) suggested that energy expenditure when accelerating in flight may be twice as great as during sustained horizontal flight. Thus the cost of flying pursuits of intruders and of those kleptoparasitic chases which involved flapping flight was assumed to be twice that of flying at V^{mr}. Kleptoparasitic chases which did not involve flapping flight were assumed to be as energetically expensive as gliding flight (3.1 times BMR). Flapping flight while patrolling between chases was assumed to take place at V^{mp} since skuas should seek to minimise energy expenditure while patrolling in front of cliffs. The cost of flight while flying to and from the cliffs was assumed to be equivalent to that of flying at V^{mr} since skuas should fly at this speed to maximise distance covered per unit energy expended.

Periods of absence from territories included actual foraging time and time spent flying to and from the foraging sites. The amount of time and energy which skuas spent per day in commuting to and from the feeding sites was calculated as follows. The average number of foraging trips made per day by each member of each pair was determined from information recorded during the hide watches. On each trip, Arctic skuas had to fly 1km to and from the cliffs while the great skuas had to fly 2km each way. The length of time which this required per trip was calculated on the assumption that the skuas flew at speed V^{mr} while commuting. These figures were multiplied by the average number of trips made per day by each bird to determine the total amount of time devoted to commuting to and from the feeding sites each day. These values were then converted to the percentages of time spent commuting, and the energetic costs were calculated assuming flight at V^{mr}.

The percentage time spent foraging was calculated by subtracting the percentage time spent commuting from the percentage time absent from the territory. The energetic costs of kleptoparasitic foraging were calculated from observations made in 1987 of the proportion of time which foraging skuas actually spent chasing, and observations made in 1986 of the proportion of chases which actually involved flapping flight and the proportion of time which skuas flapped and glided while patrolling between chases.

Kendeigh et al.(1977) pointed out that because the flight muscles generate excess heat that must be dissipated when a bird is flying,

there is no need for additional heat generation for temperature regulation during flight. Thus, flight can be considered to substitute for thermoregulatory requirements (see also Paladino and King 1984). The cost of thermoregulation at the ambient temperature during the chick-rearing period (10.89°C between 15/6 and 31/7 for Arctic skuas and 11.15°C between 15/6 and 23/8 for great skuas) was determined by interpolation (Wiens and Innes 1974) between the SMR at 0°C (Kendeigh et al. 1977 eqn 5.15) and the BMR (Kendeigh et al. 1977 eqn 5.5) at the critical temperature at which SMR=BMR (Kendeigh et al. 1977 eqn 5.12). This was then added to the metabolic costs of activity, allowing for the substitutive effect of flight on the need for generation of heat for thermoregulation.

The costs of chick maintenance and growth were calculated from equation 5.78 of Kendeigh et al. (1977). The chick weights used in these calculations were predicted on the basis of their ages mid-way between the first and last hide watches on each pair when feeding chicks. The weights of chicks of the appropriate age were calculated from the equations of logistic growth curves derived from measurements of chick growth in 1987. The data points from which these equations were derived are presented in chapter 4. To allow for the additional cost of chick thermoregulation at the ambient temperatures recorded, temperature coefficients were calculated from equation 5.21 of Kendeigh et al. (1977). These values were multiplied by the difference between ambient temperatures and temperatures in the thermoneutral

zone of skua chicks which, following Furness (1980), was assumed to be 20°C. These values were then added to those obtained for the cost of chick growth and maintenance at thermoneutrality to obtain the total daily energy budget of the young birds out of the nest.

From the calculations outlined above the total daily energy requirement of each pair was determined for an average day during the chick-rearing period.

3) Calculation of the energy reward of foraging

The energetic reward per hour of kleptoparasitic foraging was calculated from the proportion of foraging time which skuas spent chasing, the mean chase duration (from which the number of chases carried out by a single skua in one hour was calculated), the success rate in securing fish from chases, the number of fish secured per successful chase, the proportion of chases which were of each of the main host species and the average energy content of fish carried by these host species in 1987. The calorific values of the fish carried by the skuas' main host species were calculated from the lengths of fish which were collected from the various species of auk on Foula in 1987. These lengths were converted to weights by the species specific equations presented in Harris and Hislop (1978) and thence to calorific value per fish by other equations given in the same paper.

Under the assumption that all the time which adults were absent from their territory was spent in foraging (allowing for time spent commuting to and from the cliffs), (Furness and Hislop 1981), the gross energy gain per day by each pair of skuas was calculated.

Assuming an assimilation efficiency of 80% (Kendeigh et al.1977) the total assimilated input per day was determined for each pair. These values were then compared with the total energy requirements of each pair to determine whether kleptoparasitism was profitable enough to the skuas to meet their daily energy needs while rearing chicks.

Results

1) Calculation of BMR, cost of thermoregulation and cost of flight

The results of the calculations based on the equations of Kendeigh et al.(1977) are presented in Table 3.2 and the costs of flight at V^{mp} and V^{mr} are presented in Table 3.3.

2) Calculation of the cost of kleptoparasitic foraging.

In 1987, Arctic skuas spent, on average, only 10.58% of their foraging time actually chasing (Table 3.4). In 1986, 89.2% of chases by Arctic skuas involved flapping flight (see chapter 2). Thus Arctic skuas spent 9.44% of their foraging time engaged in high speed flapping flight (at a cost of 14.5 times BMR for males and 15.6 times BMR for females) and 1.14% engaged in chases without flapping flight (at a cost of 3.1 times BMR for both sexes). In 1986, Arctic skuas glided for 47.75% of the patrolling periods between chases (Table 3.5). Thus they spent 42.70% of their total foraging time gliding while patrolling (at a cost of 3.1 times BMR for both sexes) and 46.72% of the time engaged in flapping flight while patrolling (at a cost of 6.9 times BMR for males and 7.4 times BMR for females). These

figures combine to yield an estimate of the cost of kleptoparasitic foraging to male and female Arctic skuas of 5.96 times BMR and 6.30 times BMR respectively.

In 1987, great skuas spent, on average, only 6.45% of their foraging time actually chasing (Table 3.4). In 1986, 56.7% of chases by great skuas involved flapping flight (see chapter 2). Thus great skuas spent 3.66% of their foraging time engaged in high speed flapping flight (at a cost of 26.4 times BMR for males and 27.0 times BMR for females) and 2.79% engaged in chases without flapping flight (at a cost of 3.1 times BMR for both sexes). Furness (unpbl. 1988 data) found no difference between great skuas and Arctic skuas in the proportion of patrolling periods which were spent gliding. Therefore, given that like Arctic skuas, great skuas also glided for 47.75% of the patrolling periods between chases (Table 3.5), then they spent 44.67% of their total foraging time gliding while patrolling (at a cost of 3.1 times BMR for both sexes) and 48.88% of the time engaged in flapping flight while patrolling (at a cost of 12.5 times BMR for males and 12.8 times BMR for females). These figures combine to yield an estimate of the cost of kleptoparasitic foraging to male and female great skuas of 8.56 times BMR and 8.69 times BMR respectively.

3) Energetic reward per hour of kleptoparasitic foraging

In 1987, the mean duration of chases by Arctic skuas, recorded after 15/6 (the start of the chick-rearing period of the skuas studied) was

7.25 seconds (Table 3.6). Since Arctic skuas spent 381 seconds chasing per hour of foraging (10.58% of one hour), each skua made on average 52.6 chases per hour. From the host selection pattern of Arctic skuas over this same period (Table 3.7), they would have made an average of 7.05 chases of guillemots (Uria aalge), 40.50 chases of puffins (Fratercula arctica) and 5.05 chases of razorbills (Alca torda) per hour. From the success rates in securing fish from these species over this period (Table 3.7), Arctic skuas would have made on average 0.32, 4.94 and 0.74 successful chases per hour of guillemots, puffins and razorbills respectively. Arctic skuas only ever secured one fish from successful chases of guillemots and razorbills but secured an average of 1.09 fish from successful chases of puffins. Thus the gross gain of energy per hour by one Arctic skua can be represented by the equation;

$$\text{Gross gain} = 0.32.a + 5.38.b + 0.74.c, \qquad (3.1)$$

where a, b and c are the energy content of one fish carried by guillemots, puffins and razorbills respectively.

In 1987, the mean duration of chases by great skuas, recorded after 15/6 was 7.56 seconds (Table 3.6). Since great skuas spent 232 seconds chasing per hour of foraging (6.45% of one hour), each skua made on average 30.7 chases per hour. From the host selection pattern of great skuas over this same period (Table 3.7), they would have made an average of 12.53 chases of guillemots, 13.54 chases of puffins, 1.44 chases of razorbills and 3.19 chases of gannets (Sula bassana) per hour. From the success rates in securing fish from these species over

this period (Table 3.7), great skuas would have made on average 1.75, 3.79, 0.29 and 0.43 successful chases per hour of guillemots, puffins, razorbills and gannets respectively. Great skuas only ever secured one fish from successful chases of guillemots and razorbills but secured an average of 1.65 fish from successful chases of puffins and an average of 3.50 fish from successful chases of gannets. Thus the gross gain of energy per hour by one great skua can be represented by the equation;

$$\text{Gross gain} = 1.75.a + 6.25b + 0.29.c + 1.51.d, \qquad (3.2)$$

where a, b, and c are as defined above and d is the energy content of one fish carried by a gannet.

The species composition, mean lengths, weights, calorific values and energy content of samples of fish collected from auks on Foula in 1987 are presented in Table 3.8. Substitution of the mean energy content of an "average" fish carried by each species of victim, into equations 3.1 and 3.2 results in a gross energy gain of 305.60kJ/hr of kleptoparasitic foraging for an Arctic skua and a value of 599.05kJ/hr of kleptoparasitic foraging for a great skua. These calculations assume that skuas did not select victims on the basis of the size of the fish which they were carrying.

4) Balance between energy requirements and total assimilated input

During the chick-rearing period the males of pairs A, B and D/E combined foraged for 13.21, 11.20 and 13.74 hours per day respectively

while the females of the same pairs foraged for 12.87, 10.63, and 10.74 hours per day respectively (Table 3.9). With a gross gain of 599.05kJ/hr foraging and 80% assimilation efficiency pairs A, B and D/E had a total assimilated input of 12,498kJ/day, 10,465kJ/day and 11,733kJ/day respectively. These values compare with the total energy requirements of these three pairs and their chicks of; 10,375kJ/day for pair A, 7,816kJ/day for pair B and 10,101kJ/day for pairs D/E (Tables 3.10 to 3.12).

During this period of the breeding season the males of pairs A, B and D/E expended energy at rates of 5.64, 5.06 and 5.84 times BMR respectively. Over the same period the females of these same pairs had energy expenditures equivalent to 5.62, 4.95 and 4.96 times BMR respectively.

During the chick-rearing period the males of pairs X, Y and Z foraged for 8.89, 5.73 and 7.76 hours per day respectively while the females of the same pairs foraged for 6.50, 4.56 and 7.07 hours per day respectively (Table 3.9). With a gross gain of 305.60kJ/hr foraging and 80% assimilation efficiency pairs X, Y and Z had total assimilated inputs of 3,762kJ/day, 2,516kJ/day and 3,626kJ/day respectively. These values compare with the total energy requirements of these three pairs and their chicks of; 4,216kJ/day for pair X, 2,200kJ/day for pair Y and 3,341kJ/day for pair Z (Tables 3.13 to 3.15).

During this period of the breeding season the males of pairs X, Y and Z expended energy at rates of 3.93, 3.40 and 3.76 times BMR

respectively. Over the same period the females of these same pairs had energy expenditure rates equivalent to 3.63, 3.28 and 3.75 times BMR respectively.

Discussion

In recent years, the daily energy expenditure of free-living birds has been the subject of much research (see Table 3.16 for references). One of the most popular methods of calculating daily energy expenditure (DEE) has been to combine observed time activity budgets of the birds with laboratory derived, or in some cases (including the present study), literature derived, measurements of the energetic cost of the various activities recorded (Schartz and Zimmerman 1971, Tarboton 1978, Holmes et al.1979, Furness 1980, Burger 1981, Mugaas and King 1981, Finch 1984, Gaston 1985, Birt and Cairns 1987).

However, with the development of the doubly labelled water (DLW) technique, which was originally proposed by Lifson et al. (1955), many recent studies have utilised this technique to determine the daily energy expenditure of birds (see other references in Table 3.16). Some studies have used the DLW technique to test the accuracy of various time energy budget (TEB) models (Weathers and Nagy 1980, Bryant et al. 1984, Williams and Nagy 1984, Weathers et al.1984, Buttemer et al. 1986, Masman et al.1988). The results of these studies have indicated that DEEs calculated by some TEB models vary quite markedly from the values obtained by the DLW technique (Weathers and Nagy 1980, Williams and Nagy 1984, Weathers et al.1984, Buttemer et al. 1986). These

results led Weathers et al.(1984) to the conclusion that the results of "earlier time budget studies that used assumed standard metabolic rates versus ambient temperature data should be interpreted with caution, as their estimates may be in error by +/- 20-40%". They further concluded that " time budget estimates that assign to behaviours energy equivalents that have been derived from the literature rather than empirically may be no better than approximations that use existing allometric equations to predict DEE from the bird's body mass alone (Walsberg 1983) or from its mass and the mean daily air temperature (Kendeigh et al.1977)".

According to Weathers et al.(1984), one of the major errors inherent in many previous studies is the means by which the energy expended on thermoregulation was calculated. Comparison of the DEEs of loggerhead shrikes (Lanius ludovicianus) calculated by several different TEB models which differed in their method of calculation of thermoregulatory costs, indicated that only one (TB1) gave a close fit to the DEE measured by the DLW method (Weathers et al. 1984). This model calculated the cost of thermoregulation on the basis of operative temperature (T^e) rather than ambient temperature (T^a) and also took into account the effect of the wind on heat loss. The other two models which used ambient temperature and accounted for the wind, or which used operative temperature but did not account for the wind yielded DEEs 9.1% higher and 14.2% lower than the value derived by the DLW technique. These three models gave similar results when compared against DLW derived DEEs of budgerigars (Melopsittacus undulatus),

(Buttemer et al.1986).

However, in both of these studies (Weathers et al.1984, Buttemer et al. 1986) the prevalent environmental conditions were such that the ambient and operative temperatures were almost always below the lower critical temperatures of the birds concerned. Further the loggerhead shrikes and the budgerigars spent only 0.47% and 0.17-0.33% of the observation periods engaged in flight during which the need to generate heat for thermoregulation would have been obviated due to the excess heat produced by the flight muscles (Kendeigh et al. 1977, Bryant et al.1984, Williams and Nagy 1984, Buttemer et al.1986). Thus the shrikes and the budgerigars had to generate heat specifically for thermoregulation for the majority of the time. The consequences of these conditions were that the shrikes expended an average of 42% of their total DEE on thermoregulation. The corresponding figure for the budgerigars was probably similar to this value for the loggerhead shrikes. Therefore, it is not surprising that TEB models which failed to determine the cost of thermoregulation accurately, yielded markedly different results to the DLW measurements in these cases.

In the present study, the cost of thermoregulation, as calculated, did not account for more than 6% of the total DEE of skuas during the chick-rearing period. Moreover, it is felt that this figure is probably an overestimate. Furness (in press) has shown that skuas possess large quantities of insulative plumage, in relation to their mass, when compared with species of seabird which breed at lower

latitudes. In addition, skuas have thick scutes covering their legs (Furness 1987a). Furness (in press) has postulated that in comparison with gulls which have relatively fleshy legs, skuas are less able to lose heat through their legs and feet. Presumably, this could serve to reduce heat loss in cold environments. Thus, it would appear that skuas are adapted for life in the colder areas of the world. Therefore, it is not unrealistic to assume that skuas' lower critical temperatures are lower than the estimates used in this study which were predicted from the allometric equation of Kendeigh et al. (1977). Thus, although the mean ambient temperature in summer in Shetland was lower than the calculated lower critical temperatures of both species of skua, this was probably not the case in reality. Skuas may not require to generate excess heat for thermoregulation at all when breeding at latitudes as low as Shetland's. The calculated DEEs of skuas which incorporate thermoregulatory requirements may, therefore, be overestimates. Even so, the error would only be 6% at most. Similarly, it is felt that failure to account for the effect of wind on the heat loss of skuas, is probably of little importance, in comparison with the studies of the loggerhead shrikes (Weathers et al. 1984) and budgerigars (Buttemer et al.1986). This assumption is based on the fact that skuas were never above ground level when not flying, whereas the shrikes and budgerigars could perch at heights up to 3m above the ground where the effect of any wind would be greater.

Another source of error in TEB estimates of DEE which was pointed out by Weathers et al.(1984), was the use of standard metabolic rates

derived from the literature or allometric equations such as those of Kendeigh et al.(1977). Weathers et al.(1984) found that a TEB model which incorporated SMR data from a population of shrikes other than the one under study, resulted in the DEE being overestimated by 22.2%. However, the reason for this discrepancy was that the shrikes which were being studied were not in their thermoneutral zone most of the time. Had they been so, then given the difference of only 2.7% in the BMRs of the two populations of shrikes, it is unlikely that the use of data from the other population of birds would have made such a difference to the results. It is unlikely that skuas in Shetland ever experienced temperatures below their lower critical temperature, or for that matter, above their upper critical temperature. Thus, the use of SMR and BMR values derived from the equations of Kendeigh et al. (1977) with modifications based on the results of Ricklefs and Matthew (1983), probably did not result in serious errors in the DEEs which were calculated.

The third source of error in the calculation of DEEs which was discussed by Weathers et al. (1984) was the use of energetic equivalents of behaviours derived from the literature rather than empirically. During the chick-rearing period, the only two behaviours which skuas regularly indulged in were resting and foraging. These two behaviours usually accounted for 85% or more of the skuas' day. Hence, only errors in the energetic equivalents assigned to these two behaviours were likely to have influenced the DEEs which were

calculated.

Weathers et al. (1984) found empirically that the cost of alert perching was 1.98 times BMR and assumed that the cost of perching at night was equivalent to BMR if ambient temperature exceeded the lower critical temperature. The estimated cost of resting used in this study (1.5 times BMR) seems realistic in view of these figures. This leaves the estimated cost of foraging as the only major source of error in the calculation of the skuas' DEEs.

Bryant et al.(1984) found that their estimates of DEE by the time energy budget method were most sensitive to errors in the cost of flight. This was presumably because the two study species spent between 20% and 56% of their time flying. Measurements of the cost of flight in free-living birds have been made in only a few studies (Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984, Westerterp and Bryant 1984, Adams et al.1986, Costa and Prince 1987, Masman and Klaassen 1987, Obst et al.1987). All of these studies, with the exception of Masman and Klaassen (1987), have indicated that the cost of flight is less than the commonly used figure of 12 times BMR. The subjects of all these studies (with the exception of Masman and Klaassen (1987)) were very aerial species. Hails (1979) pointed out that species such as hirundines (Order Passeriformes Family Hirundinidae) and swifts (Order Apodiformes) which are constantly on the wing when foraging would be expected to have a lower cost of flight in comparison with other groups (see also Masman and Klaassen 1987). Low flight costs can be achieved with the aid of morphological

adaptations to reduce power requirements (Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984, Adams et al.1986, Costa and Prince 1987, Masman and Klaassen 1987, Obst et al.1987). However, the low cost of flight found in these studies probably also reflects the use of inexpensive gliding or soaring flight instead of more costly flapping flight (Hails 1979, Bryant et al.1984, Adams et al. 1986, Costa and Prince 1987, Obst et al.1987). Nonetheless, sooty terns (Sterna fuscata) which used flapping flight approximately 95% of the time when winds were light, were found to have much lower costs of flight than values predicted by theoretical calculations such as those of Pennycuick (1975), (Flint and Nagy 1984). Obst et al.(1987) found similar discrepancies between measured and calculated flight costs of Wilson's storm-petrels (Oceanites oceanicus) which do not glide at all while foraging (Pennycuick 1982). Skuas, however, do not have low wing loadings or particularly high aspect ratios (see chapter 6) and hence differ from those species such as hirundines and sooty terns in which flight costs are lower than expected. Hails (1979) noted that, excluding hirundines, most of a variety of other species of bird had flight costs in the region of 12 times BMR. Masman and Klaassen (1987) found that the cost of flight in free-living European kestrels (Falco tinnunculus) was greater than 12 times BMR. Thus when considering the cost of flapping flight in species which are not aerial foragers, the equations of Pennycuick (1975) and other similar theoretical calculations may yield more realistic estimates of the cost of

flapping flight than the results of Flint and Nagy (1984) imply. Indeed the TEB model of Weathers et al.(1984) which differed from the DLW measured energy expenditure by only 0.1%, utilised a cost of flight of 13.2 times BMR which was calculated from just such theoretical equations.

In the light of these results it is felt that the estimated costs of foraging used in this study, which were derived from the equations of Pennycuick (1975) and which take into account the extensive use of gliding flight by the skuas, do not represent a large source of error in the present analyses.

The calculation of the energy balance between requirements and assimilated input revealed that two of the three pairs of Arctic skuas obtained enough food to meet their own energy requirements as well as those of their chicks. However, this was not the case for the pair, (pair X), which reared an extra chick in addition to both of their own. It would appear that with the kleptoparasitic success rate which great skuas achieved in 1987, this feeding technique would have provided energy at a sufficiently high rate to meet their own and their chicks energy requirements, had they fed entirely in this way.

However, since the energetic reward per successful chase was calculated on the basis of the energy content of a very small sample of fish collected in 1987, the values for net assimilated input per day should be viewed with some caution. In order to investigate the extent to which values for assimilated input could vary depending on the energy reward per chase, it was decided to recalculate the energy

assimilated per day by skuas under the assumption that the auks were carrying fish of the modal size collected from them on Foula between 1971 and 1980 (Furness unpbl.). Under these assumptions, none of the pairs of skuas assimilated sufficient energy per day to meet their own and their chicks' energy requirements (see figures in parentheses in Tables 3.10 to 3.15). Obviously the estimated energy contents of the fish which are used in calculations such as these, greatly influences the results obtained and the conclusions which may be drawn from them. The main reason for the differences in the results of these two sets of calculations was that the fish which were collected from puffins and razorbills in 1987 were larger than the modal length of fish carried by these two species between 1971 and 1980. It might, therefore, be argued that the positive energy balance for the skuas was due solely to the collection of fortuitously large fish from puffins and razorbills in 1987. Several studies have shown that kleptoparasites tend to selectively chase victims with larger than normal prey (Hopkins and Wiley 1972, Hatch 1975, Arnason and Grant 1978, Thompson 1986). Thus, samples of fish collected by observers may be biased towards smaller fish sizes than those which the skuas were actually stealing. The fish stolen by skuas in 1987 might, therefore, have been larger and hence more energy rich than those collected. If this were true then the skuas would have been assimilating more energy per day than was calculated in the first place.

Clearly the relationship observed between daily energy expenditure and net assimilated input per day for each pair of skuas is heavily dependent on the values assigned to various parameters in the calculations, not least of which is the energy content of the auks' fish. Thus the values presented in Tables 3.10 - 3.15 cannot be regarded as absolute rates of energy expenditure and assimilation. However, bearing in mind the imprecise nature of these calculations, especially those of the net energy assimilated per day, it appears that kleptoparasitism was a profitable feeding technique to Arctic skuas (rearing normal sized broods), and a feeding technique which would have been profitable enough to allow great skuas feeding entirely in this way to breed successfully.

From the foregoing discussion it is obvious that the sizes of fish carried by auks in any given year have a large influence on the energy balance of skuas. If auks were to return to their chicks with smaller fish in any one year, the skuas' energy balance would become negative unless they altered their time budgets and foraged more in order to compensate. This would be true even if the size of fish carried by the auks decreased only slightly since the calorific value of fish increases exponentially with fish length (Harris and Hislop 1978). This is partly because large fish have a relatively greater fat content than smaller fish of the same species (Harris and Hislop 1978).

Only a few studies have been carried out on the energy balance of kleptoparasites feeding offspring (Arnason and Grant 1978, Furness 1980, Burger 1981). In accord with the present study, Furness (1980) found that one pair of Arctic skuas breeding on Foula assimilated a sufficient quantity of energy per day to meet their own and their chicks' energy requirements. However, this was not true of Arctic skuas in Iceland (Arnason and Grant 1978). Arnason and Grant (1978) found that the Arctic skuas' rate of food intake was not sufficient to meet their own energy requirements (let alone those of their chicks) during certain weeks of the breeding season. Burger (1979) found that chick survival of lesser sheathbills between hatching and fledging averaged 56% and that the major cause of chick-death was starvation. In the light of these findings, Burger (1981) suggested that during temporary food shortages, lesser sheathbills may have had insufficient time to meet their own food requirements as well as those of their chicks. Burger (1981) further concluded that without access to penguins or other colonial seabirds, lesser sheathbills would probably be incapable of rearing chicks at his study site. Furness (1980) came to a similar conclusion regarding the importance of kleptoparasitism to the breeding success of Arctic skuas in Shetland. As mentioned previously, great skuas in Shetland obtain very little of their food kleptoparasitically. However, the results of the present study clearly indicate that this feeding technique represents a profitable alternative to which great skuas could turn in the event of other

food sources becoming less readily available. Recent studies (Hamer, Furness and Caldow in prep.) indicate that in response to the reduction in the availability of sandeels around Shetland in recent years, great skuas have indeed changed their diet. There is little direct evidence as yet to suggest that great skuas are behaving more kleptoparasitically than in the past. However, in 1988 the proportion of great skuas' diet which consisted of seabirds was much higher than before (Hamer, Furness and Caldow in prep.). This may be indirect evidence that great skuas were behaving more kleptoparasitically than before since victims of kleptoparasitic chases are sometimes caught by great skuas.

Current theory suggests that optimal reproductive tactics serve to maximise each individual's lifetime reproductive value; this being the sum of all present plus all expected future offspring (Pianka 1976). Further, there should be an inverse relationship between the reproductive effort expended in any one year and residual reproductive value (a measure of the expectation of future offspring) if reproductive effort subjects the breeding organism to risk (Goodman 1974). The results of a wide range of empirical studies (reviewed by Reznick 1985) support this assumption that there are costs to high levels of reproductive effort. The majority of these studies have been carried out on organisms other than birds. Two recent experimental studies on birds which involved the manipulation of brood sizes (Nur 1984, Reid 1987) both found evidence of an increased cost to adults in terms of decreased survival after increased reproductive effort.

Where a species is capable of iteroparity (ie repeated reproductive episodes within a lifetime), an individual's lifetime reproductive success may be maximised by employing a conservative breeding strategy in which reproductive effort in any one year is low in order to maximise the likelihood of survival to reproduce in the future (Williams 1966). Generally speaking, seabirds are long-lived, iteroparous species which exhibit just such conservative breeding strategies. Goodman (1974) lists the conservative traits of offshore-feeding seabirds as "small clutch size, long incubation period, long fledging period, long reproductive cycle, delayed replacement of lost egg or chick , deferred maturity, and abandonment of the breeding attempt under stress". This last conservative trait listed by Goodman (1974) as characterising offshore-feeding seabirds is particularly interesting given the environmental conditions prevalent during the 1987 breeding season in Shetland and the calculated DEEs of the skuas.

Drent and Daan (1980) concluded that the maximum daily work capacity of birds during the breeding season is approximately 4 times BMR. In the vast majority of the studies of the daily energy expenditure of free-living birds, the calculated DEEs have indeed been below this critical value (see Table 3.16). However, in the present study all the great skuas had DEEs during the chick rearing period in excess of 4 times BMR, and higher than the vast majority of previously studied species (Table 3.16). These results might indicate some flaw in the method employed in this study to calculate the DEEs, but the fact that

the DEEs of all six Arctic skuas, (even ones which were rearing three chicks), which were calculated in exactly the same way as those of great skuas, were less than 4 times BMR argues against this. Although the cost of foraging by great skuas was calculated on the unrealistic assumption that they were feeding entirely by kleptoparasitism, it is felt that this does not represent an overestimate of the actual foraging costs of great skuas given the large amount of soaring and gliding which was incorporated in the calculations. The implication of these findings is that in 1987, great skuas were indeed expending a great deal of energy in an attempt to rear their chicks. This is surprising given that great skuas usually have very high adult survival and are long-lived (Furness 1987a).

It has been argued that it is not possible to use ratios of DEE to BMR as a measure of reproductive effort (Bryant et al. 1984). The reason for this is that parental investment in reproduction can take the form of energetically expensive activities such as foraging to collect food for the offspring or alternatively energetically inexpensive activities such as vigilance to deter predators. Since vigilance can be achieved without moving, an hour devoted to guarding the young would be much less energetically expensive than an hour spent foraging, yet potentially just as useful in ensuring reproductive success. Finch (1984) found that female Abert's towhees spent considerable amounts of time at the nest even during the nestling period. She concluded that this served both to conserve energy while at the same time placing the female in a position to

protect the young from predation. By sitting on the nest, the female towhees actually exposed themselves to the risk of predation, (Finch 1984). Thus the risks which they took in an attempt to rear their young (a measure of reproductive effort) were probably higher than if they had spent more time foraging instead, even although they reduced their DEE and hence DEE to BMR ratio by behaving as they did.

The high ratio of DEE to BMR exhibited by the great skuas may not, therefore, represent an abnormally high level of parental investment. The results may merely reflect the fact that great skuas were devoting a great deal of their time to energetically expensive activities such as foraging rather than inexpensive chick-guarding. Even so, the question remains as to why great skuas opted to invest so much of their time in foraging.

In the normal course of events, male great skuas carry out most of the foraging when the chicks are small while the task of guarding the chicks falls to the females which remain on their territories. As the food requirements of the growing chicks increase , male great skuas forage more and the females take an increasing part in the collection of food (Furness 1987a). The same pattern of role differentiation between the sexes is apparent in Arctic skuas in Shetland (Furness 1980), and is typical of many raptorial species of birds such as hawks (Order Falconiformes) and owls (Order Strigiformes) which, like skuas, show reversed sexual size dimorphism. In the past, skuas were always able to synchronise their foraging activities such that chicks were

never left unguarded (Furness and Hislop 1981). In 1987, this was no longer the case for great skuas (see chapter 4). Presumably, food availability in the past was sufficiently high to enable males to meet the major part of the food requirements of the chicks by themselves, which in turn allowed the females to remain on their territories and protect the chicks while their mates foraged. Intuitively, the likelihood of chicks starving to death when they are not fed often enough exceeds that of unguarded chicks being killed. When food availability was high this was probably of little importance since a pair could gather sufficient food without having to take the risk of leaving their chicks. However, from observations in 1986 and 1987, it was apparent that the reduction in the availability of sandeels has forced great skuas to take the "gamble" of leaving their chicks unguarded in order to try to supply sufficient food to maintain chick growth and survival. There is little point in protecting chicks which are dying of starvation. That there has been a change in the trade-off between guarding chicks as opposed to feeding them is evinced by the fact that it was female great skuas, which normally play the major part in guarding the offspring, that increased their foraging effort most in 1987 relative to the situation in the past (10.6-12.9 hours per day foraging in 1987 compared to a maximum of 5 hours per day in 1976 (Furness 1987a)). This same trend is apparent in the Arctic skuas time budgets. In 1987 the female Arctic skuas spent between 4.6 hours and 7.1 hours foraging per day compared to an average (over the chick-rearing period) of 4.1 hours per day in 1979

(Furness 1980). The poor breeding success of great skuas in 1987 (see chapter 4) would seem to indicate that this "gamble" did not pay off. Not only did great skuas in 1987 fail to sustain their previously high level of breeding success, but they also expended much more effort in their attempt than would be expected of such a long-lived species. It is difficult to reconcile these findings of apparent "risk taking" by great skuas with the idea that the optimal reproductive tactic of a species in which iteroparity is a possibility, is to favour adult survival in preference to the success of any given reproductive attempt. Perhaps the cost of reproduction to great skuas in 1987 was not sufficiently high (in spite of the rate of daily energy expenditure exceeding 4 times BMR) to merit the abandonment of their breeding attempts. However, should the availability of food decrease further in the future, great skuas may abandon their breeding attempts as the reduction in residual reproductive value, caused by increased energetic costs of prolonged foraging, outweighs the benefits of increased investment in present offspring.

Chapter 4

Territorial attendance patterns and breeding biology of skuas.

Introduction

Skuas, like all seabirds, have to come to land to breed, and like many species each breeding pair occupies a territory in which they make their nest, lay their eggs, and rear their chicks.

Unlike most species of seabird which defend small areas around the nest, within which they do not forage (Type C territories of Hinde 1956 and Perrins and Birkhead 1983), some populations of skuas also forage within their territories and are said to hold "all-purpose" territories (Type A territories of Hinde 1956 and Perrins and Birkhead 1983). For example Arctic skuas (Stercorarius parasiticus), long-tailed skuas (Stercorarius longicaudus) and pomarine skuas (Stercorarius pomarinus) which breed in Alaska hold "all-purpose" breeding territories in which they hunt for microtine rodents, small passerines, bird eggs, and insects (Maher 1974). The size of the territories held varies between years depending on the prey availability; pomarine skuas breed at a range of densities between 0.1 and 13.7 pairs per km^2 according to the abundance of brown lemmings (Lemmus lemmus), while long-tailed skuas breed at densities between 0.1 and 1.7 pairs per km^2 (Furness 1987a). The skuas appear to assess prey availability as they set up their territories each year and defend an area which is sufficiently large to contain enough prey to

meet future requirememts. Furness (1987a Fig 74) showed that nesting densities of skuas (and hence territory sizes) depend on whether they feed predominantly within or outside their territories (see also Pietz 1987). In Shetland, Arctic skuas and great skuas (Catharacta skua) breed at high densities (20-200 pairs per km^2 and c50-over 1000 pairs per km^2 respectively) and thus hold small breeding territories which contain very little food. Hence, although both species have been recorded feeding on crowberries (Empetrum nigrum) and occasionally on small passerine birds which occur in their territories (Furness 1980), they forage almost entirely out at sea. In Shetland, Arctic skuas and great skuas hold Type C territories (Hinde 1956, Perrins and Birkhead 1983) typical of many seabirds.

In Shetland, skuas spend very little time away from their territories engaged in activities other than foraging (Furness and Hislop 1981), thus here at least, it should be possible to use the territorial attendance patterns of breeding great skuas and Arctic skuas as an indicator of parental foraging effort. Furness and Hislop (1981) found that the time spent in foraging at sea by great skuas correlated with dietary composition, and they argued that great skuas have to work harder to obtain sufficient food if their preferred prey is unavailable. O'Donald (1983) argued that Arctic skua breeding numbers in Shetland could not be limited by food supplies because they spend very little time each day foraging and much time sitting on the territory which he assumed could be devoted to foraging at sea if the birds wished to increase the rate of provisioning the chicks. Even so,

as pointed out by Furness and Hislop (1981) in reference to great skuas, any change in the availability of Arctic skuas' prey should cause a change in their foraging effort. Hence territorial attendance patterns can be used to study food availability.

In this chapter I describe the territorial attendance patterns of great skuas and Arctic skuas on Foula and examine the ways in which these are related to timing of breeding, stage of the breeding cycle, brood size and food availability. Various other aspects of the breeding biology of skuas are discussed in relation to territorial attendance patterns.

Methods

1) Territorial attendance patterns

In 1986 the territorial attendance patterns of nine pairs of Arctic skuas and nine pairs of great skuas were studied from June until August while in 1987 twenty eight pairs of Arctic skuas and twenty seven pairs of great skuas were studied from April until August. The territorial attendance of the study pairs was recorded by making spot observations of the number of adults on each territory at least once, and usually twice, every day between 09.00 BST and 21.00 BST. Skuas in Shetland feed only during daylight (Furness 1987a), thus all observations were made during the period when skuas could have been foraging. For any given spot observation on any given pair, the territorial attendance value could be one of three possible scores:

0. Neither adult of the pair was present on the territory.

1. Either the male or the female of the pair was present on the territory while its mate was absent.

2. Both adults of the pair were present on the territory.

If the territorial attendance patterns of skuas in Shetland are indicative of parental foraging effort, then territorial attendance values will be influenced by factors which affect the amount of foraging which breeding birds have to do. Foraging effort might be expected to vary with the stage of the breeding season, according to whether birds are incubating or have small or large chicks to feed and also to vary with the number of chicks which a pair has to feed. Foraging effort may also be influenced by laying date, and by variations in food availability within and between seasons. In order to determine whether skuas' territorial attendance patterns varied, within each period of the breeding cycle, with their laying date or between different periods in the breeding cycle it was necessary to divide the season into the various stages. Thus it was essential to determine the dates of egg-laying, egg-hatching and chick-fledging for each pair.

In 1986, territorial attendance scores were not recorded until mid-June by which time all pairs were either incubating or had chicks to feed. Because no observations were made prior to egg-laying, there was no need to determine the laying dates for the purpose of splitting observations into pre and post egg-laying periods. The hatching dates

of 9 of the 18 pairs studied in 1986 were determined by direct observation, and that of one pair by subtraction of the appropriate fledging period (see below) from the observed fledging date. The hatching dates of the remaining 8 pairs studied in 1986 were not determined either because their chicks were never seen to fledge (and hence hatching dates could not be determined by subtraction of the appropriate fledging period) or else because the observed fledging date indicated that territorial attendance scores had been recorded only during the latter part of the pre-fledging period such that there was no possibility of including observations made during the early part of the pre-fledging period (see below). Fledging dates were determined by direct observation of chicks flying.

In 1987 a much more detailed study of territorial attendance was carried out and more rigorous techniques were employed to determine laying, hatching and fledging dates. To avoid disturbance to the birds no attempt was made to record laying dates by direct observations which would have required repeated visits to each territory. The only pairs whose laying dates were determined by direct observation were those pairs whose time-budgets were studied by hide watches (see chapter 3) on the day on which they happened to lay, and a few other pairs whose marked change in aggressive behaviour from one day to the next prompted a search of their territory for eggs.

On one occasion during the incubation period the nest of each pair was visited. On inspection of nests, if a single egg was found it was marked A with an indelible marker while if two eggs were found they

were marked A and B. The length and breadth of each egg was measured to the nearest 0.05 mm using Vernier callipers and egg' weights were measured to the nearest 0.25 g using a Pesola spring balance. Total egg volume (V) (cm^3) is given by the equation,

$$V = K_v.LB^2, \qquad (4.1)$$

where L is egg length (cm), B is egg breadth (cm) and K_v is a shape constant with value 0.507 (Hoyt 1979). Egg density (D) is then given by the equation,

$$D = W/V, \qquad (4.2)$$

where V is the total egg volume (cm^3) and W is egg weight (g). By reference to conversion figures for great skua and Arctic skua eggs (Furness and Furness 1981), the percentage of incubation completed prior to weighing was determined for each egg, from their measured densities. Assuming an incubation period of twenty six days for Arctic skuas (O'Donald 1983) and twenty nine days for great skuas (Cramp and Simmons 1983), the hatching date of every egg was predicted to within two or three days (Furness and Furness 1981). The nest of each pair was revisited around the predicted hatching time and exact hatching dates determined by direct observation if the visit was timed correctly. The laying dates of these pairs were then determined by subtraction of the appropriate incubation period from the date of hatching of the first chick. The laying dates of pairs with clutches of two of which the second-laid egg (as determined by its density) was the only one to hatch, were determined as described above, but

allowing for an additional two days of incubation of the first egg before the laying date of the second egg.

For those pairs whose hatching dates were not directly observed and whose laying date could not be derived therefrom, it was necessary to use another technique to determine these dates. In 1987 chicks of the study pairs were weighed and measured at intervals of between four and eight days throughout the pre-fledging period. Weights were measured to the nearest 5 g using a Pesola spring balance and wing lengths (maximum chord) were measured to the nearsest 1 mm using a steel wing rule. Where chick ages were not known by direct observation of hatching dates, these were determined by reference to growth curves of wing length against age, derived from chicks of known age, which are presented in Furness (1977) and Furness (1980). Thus from measurements of chicks it was possible to determine their ages and hence their hatching dates and thence by subtraction of the appropriate incubation period from the estimated hatching dates, the laying dates of those pairs for which neither hatching nor laying dates had been determined by direct observation.

The laying dates of the 55 pairs of skuas which were studied in 1987 were determined/estimated as follows;

1. Determined by direct observation - 5 pairs.

2. Estimated from measured egg densities - 3 pairs (whose eggs failed to hatch).

3. Estimated from observed hatching date by subtraction of appropriate incubation period - 22 pairs.

4. Estimated from hatching date, which had been previously estimated from wing-length measurements of chicks, by subtraction of the appropriate incubation period - 25 pairs.

The hatching dates of the 52 pairs whose eggs began to hatch were determined/estimated as follows;

1. Determined by direct observation - 27 pairs.
2. Estimated from wing-length measurements of chicks - 25 pairs.

The fledging dates of the pairs studied in 1987 were determined either by assuming a fledging period of thirty days for Arctic skuas and fifty days for great skuas (these are towards the upper end of the range of fledging periods given in Cramp and Simmons 1983), or by direct observation of chicks flying. In practically all cases these two techniques produced dates which agreed to within a day or two although the observed fledging dates did occasionally predate the predicted date by a few days.

The pre-fledging period was divided into two parts for the analysis of the attendance data; the first fourteen days after chick hatching for great skuas and the first eight days after chick hatching for Arctic skuas, and the remainder of the pre-fledging period. The reason for this is that the increase in chick weight with age for chicks of both species follows a logistic growth curve (Furness 1977, Furness 1980, Furness 1987a). During the first twelve to fourteen days after hatching, and the first six to eight days after hatching, the rate of weight increase of great skua and Arctic skua chicks respectively is

not as rapid as it is later. Thus parental foraging effort and hence territorial attendance might be expected to change between the early stages and later stages of the pre-fledging period.

In order to determine the effect of the number of chicks being fed, on parental foraging effort it was essential to determine the brood size of each pair and to determine if and when chicks died in order to exclude pairs from analysis as soon as any of their chicks died. Skua chicks, being precocious, remain in the nest for only a few days after hatching (Furness 1987a) and thereafter wander freely within their parents' territory and spend most of the time hiding in hollows or between/under clumps of vegetation. Since skua chicks, particularly those of Arctic skuas are cryptically coloured, it was not always possible to find chicks when territories were searched, and hence brood sizes could not always be determined precisely.

Pairs which laid only one egg, which subsequently hatched, obviously had a brood size of one, and pairs which laid two eggs both of which hatched obviously had a brood size of two. However, pairs which laid two eggs yet were only ever found to have one chick on their territory could have had a brood size of either one or two. The brood size of such pairs was considered to be one if either of the two following situations occurred:

1. The second-laid egg hatched first. (In this case the other egg was assumed not to have hatched (see Furness 1977)).

2. During the pre-fledging period the same single chick was found on three consecutive visits to the territory. (In this case the other egg was assumed not to have hatched or the chick to have died very young).

The dates of chick death were determined as accurately as possible by observing changes in the adults' behaviour which indicated that their breeding attempt had failed and by regularly checking each territory for the remains of dead chicks. This was done , usually with binoculars, from outwith the study territories. In several instances chicks were never found dead but simply "disappeared". In both these situations, attendance data for these pairs, which was recorded during the period of the breeding cycle in which their chicks "disappeared" or were found dead, were excluded from the analysis. In this way, attendance data for a given pair during a given stage of the breeding cycle was only analysed if the pair were known to have successfully completed that stage. The attendance patterns of great skuas and Arctic skuas were analysed separately and data for 1986 and 1987 were also kept separate. The analyses of 1987 data were carried out as follows.

The sample of pairs studied was divided into groups according to whether they had laid on or before the mean laying date, or thereafter, and whether they had a brood size of one, or two. The mean territorial attendance value for each pair was determined by summing all the spot observation scores made on that pair and dividing by the total number of spot observations. This was done separately for each of the following periods of the breeding season:

1. The pre-laying period (ie from the 23rd of April until the date of egg-laying). For all pairs of skuas the pre-laying period, as defined here, represented between five weeks and two weeks prior to laying. For 22 of the 27 pairs of great skuas and 16 of the 28 pairs of Arctic skuas, the pre-laying period represented either the four or three weeks prior to laying. Only observations made after both members of a pair had returned to their territory were included in the dataset.

2. The incubation period.

3. The first fourteen days post-chick-hatching for great skuas or the first eight days post-chick-hatching for Arctic skuas.

4. The remainder of the pre-fledging period.

5. The post-fledging period.

The effect of laying date on attendance was determined by comparing the attendance, during each period, of pairs which had the same brood size but which had laid either on or before the mean laying date, or that had laid thereafter. The effect of different brood sizes was determined by comparing the attendance, during each period of the breeding season, of pairs with different brood sizes. The effect of changing food requirements on the adults foraging effort was determined by comparing attendance, recorded in successive periods of the breeding season, for pairs of each brood size.

These comparisons were carried out by means of Mann-Whitney U tests between the two appropriate independent groups with the mean territorial attendance value of each pair being one case.

Unfortunately the number of pairs which were studied in 1986 was too small to allow the effect of laying date on attendance to be determined. Apart from this, the analysis of the mean territorial attendance values recorded in 1986 was carried out in the same manner as was employed for the 1987 data.

The spot observation data recorded in 1987 were also used to determine values for the following parameters for each day, for pairs with broods of one and pairs with broods of two:

1. The percentage of all adults present on their territories during spot observations.

2. The percentage of occasions on which both adults of a pair were seen together on their territory.

3. The percentage of occasions on which both adults of a pair were absent from their territory at the same time.

As before, these data were divided into the pre-laying period, the incubation period, the early and late pre-fledging periods and the post-fledging period (on the basis of the mean laying date, hatching date and fledging date in this case). The data were then analysed in a similar manner to that described above (ie by Mann-Whitney U tests between the appropriate independent groups), in order to investigate differences in attendance patterns, within each period, between pairs with different brood sizes and between periods for pairs with a given brood size. However, in these comparisons one case represented the observations made on one day.

In order to investigate any differences in attendance patterns between years, the mean territorial attendance values, during each period of the breeding cycle, recorded in 1986 and 1987 were compared for pairs of both brood sizes. Again these comparisons were carried out by means of Mann-Whitney U tests with the two years being the independent groups. Comparisons of the data recorded in 1986 and 1987 were then made with data collected on Foula in the 1970s. In 1976 the mean territorial attendance values during the latter part of the pre-fledging period were recorded for two pairs of great skuas with one chick and two pairs with two chicks (Furness and Hislop 1981). Mann-Whitney U tests were again used in these comparisons. In 1979 spot observations of territorial attendance were carried out on a number of pairs of Arctic skuas of known brood size (Furness 1980). Furness (1980) did not use these data to calculate the mean territorial attendance values for each pair, but pooled observations made on an unspecified number of pairs and presented the data as the number of occasions on which either one or two adults were seen on their territory. Data collected in 1986 and 1987 were converted to the same form and chi-square tests carried out.

One potential problem in the analysis of the territorial attendance data outlined below, is the possibility of obtaining statistically significant results by chance, as a consequence of carrying out many tests on one dataset, of which one in twenty might be expected to give a spurious "significant" result. However, the separate analysis of 1986 and 1987 data and comparisons between species provide an

opportunity to detect any misleading results, and the direction of any trends can be predicted on the basis of biological common sense.

2) Breeding biology

In 1987, various aspects of the breeding biology of the study pairs of skuas were investigated. These were then compared with similar data recorded on Foula in the 1970s (Furness 1977, 1980), as a parallel approach to the comparison of territorial attendance patterns between these years.

The mean laying dates of the sample of great skuas and Arctic skuas were calculated from the laying dates which were determined as described above. The mean clutch sizes of skuas in 1987 were compared with those of skuas which bred in the 1970s by chi-square tests of the proportion of pairs which laid one or two eggs. For comparison with the studies of Furness (1977,1980), mean internal egg volumes (V_i) (cm^3) were calculated from the length and breadth of eggs by the equation,

$$V_i = 0.00048.L.B^2, \qquad (4.3)$$

where L is egg length (mm), B is egg breadth (mm) and 0.00048 is a constant (Coulson 1963, Coulson et al. 1969). Internal egg volumes of skuas in 1987 were compared, by means of d-tests, with those of great skuas in 1975 (Furness 1977) and those of Arctic skuas in 1979 (Furness unpbl.).

Because the nests of study pairs were not visited daily in 1987, and because of the precocious nature and cryptic appearance of skua

chicks, exact figures for hatching success and fledging success were not determined in 1987. Instead maximum and minimum values for these parameters were determined (as in Furness 1980) allowing for the possible fates of those eggs and chicks which were of unknown status. The assumptions used in determining the possible fates of such eggs/chicks were as follows:

1. In a clutch of two, if the second-laid egg (as determined by its density) hatched first, then the other egg was assumed to have failed to hatch.

2. If the second-laid egg in a clutch of two was not beginning to hatch on the predicted hatching day of the first-laid egg, it was assumed that it could have hatched subsequently, even if only the same single chick was found on all subsequent visits to the territory.

3. A skua chick which "disappeared" prior to the minimum fledging age (25 days for Arctic skuas and 40 days for great skuas (Cramp and Simmons 1983)), and that was not seen at all after the expected fledging date, was assumed not to have fledged.

4. Any chick which was seen alive after the minimum fledging age could have fledged.

5. Any Arctic skua fledgling which "disappeared" within the first week after fledging was assumed to have failed to survive to the end of the season. Furness (1980) stated that Arctic skua fledglings normally remain on their territories for three weeks after fledging.

Maximum and minimum hatching and fledging rates and rates of post-fledging mortality (in the case of Arctic skuas) were compared with the results of Furness (1977) and Furness (1980) by means of chi-square tests.

The logistic growth curve of great skua chicks growing "typically" (Furness 1977, Furness 1987a), was superimposed on the plot of chick weight against age derived from measurements made in 1987. Since such curves are effectively lines of best fit, it would be expected that if the chicks were growing as "well" in 1987 as in 1975, that half of the points would fall above and half would fall below this line. Thus the growth rates of great skua chicks in 1975 and 1987 were compared by means of chi-square tests of the proportion of points observed and expected to fall above and below the line of "typical" chick growth. Only measurements of chicks which hatched on or before the 20th of June were used in these analyses in order to be directly comparable with the data from which the growth curve was originally derived by Furness (1977). Furness (1980) presented data for Arctic skua chick weight in relation to age, but did not fit a curve to this data due to small sample sizes. To allow comparison between chick growth in 1979 and 1987, a line of best fit was drawn by eye through the plot of data points (Furness 1980 Appendix 5 Figure 5.3) and this was superimposed on the plot of chick weight against age for 1987. Arctic skua chick growth in 1987 was compared with that in 1979 as described above for great skuas.

3) Seabird population changes on Foula between 1976 and 1987

The data presented in Table 4.20 are from Furness (1987c). The methods involved in the collection of these census data are outlined in Furness (1981b). The total numbers of birds which were available to skuas to chase were calculated directly from the census totals.

RESULTS

1) Effect of laying date on territorial attendance

a) Pre-laying period

Analysis of the data collected in 1987 (Table 4.1) shows that only in the case of Arctic skuas with one chick did territorial attendance vary significantly with laying date, during the pre-laying period. In this case it was the later-laying pairs which had the higher attendance values.

b) Incubation period

During the incubation period there were no significant differences in territorial attendance due to laying date in either species (Table 4.1).

c) Early pre-fledging period

Territorial attendance during the early part of the pre-fledging period, differed significantly with laying date for pairs of great skuas and Arctic skuas with two chicks (Table 4.1). Late-laying pairs had lower attendance scores. This trend, although not statistically significant was also apparent among pairs with one chick.

d) Late pre-fledging period

Territorial attendance during the rest of the pre-fledging period did not differ significantly between pairs laying on or before the mean laying date and those laying thereafter (Table 4.1). These results are almost certainly a consequence of the small samples of pairs which laid after the mean laying date because in all four comparisons the trend was for the territorial attendance of later-laying pairs to be lower than that of pairs which laid earlier.

It was felt that, even although the trend of later-laying pairs to have lower territorial attendance scores than early-laying pairs during the chick-rearing period, was not statistically significant in all cases, it was necessary to carry out separate analysis of the territorial attendance patterns of these two groups in order to avoid any spurious results or confounding effects which might otherwise have arisen.

2) Effect of brood size on territorial attendance

Among pairs which laid on or before the mean laying date there were no significant differences between pairs with different brood sizes in terms of mean territorial attendance values (Tables 4.2 and 4.3), the percentage of adults on their territories (Tables 4.4 and 4.5), the percentage of occasions on which two adults were present on their territory (Tables 4.6 and 4.7) and the percentage of occasions on which no adults were present on their territory (Tables 4.8 and 4.9) during the pre-laying period, the incubation period and the early part of the pre-fledging period. This was also the case among pairs which

laid after the mean laying date (Tables 4.2 to 4.9), although the percentage of adult great skuas with two chicks which were present on their territories during the early part of the chick-rearing period was significantly lower than pairs with only one chick (Table 4.5). The reason for this result was that the percentage of occasions on which both adults of a pair with two chicks were seen together on their territory was significantly lower than pairs with only one chick (Table 4.7).

During the rest of the pre-fledging period the percentage of adult great skuas with two chicks present on their territory was significantly lower than pairs with one chick (Table 4.5). This was true both among pairs which laid on or before the mean laying date and those that laid thereafter. Although the mean territorial attendance values of pairs of great skuas with different brood sizes did not differ significantly during this period (Table 4.3), the trend was in the same direction. During the post-fledging period the percentage of adult great skuas with two chicks which had laid on or before the mean laying date that were present on their territory was significantly lower than pairs with one chick (Table 4.5). The fact that this was not true of pairs that laid after the mean laying date is of little importance given the small number of days of observation on these pairs. Similarly the fact that among pairs of great skuas which laid on or before the mean laying date, the mean territorial attendance value during the post-fledging period was not significantly

lower among pairs with two chicks than among pairs with one chick is probably a reflection of the small number of pairs studied (Table 4.3), since the trend is in the same direction.

During the latter part of the pre-fledging period neither the mean territorial attendance values nor the percentage of adult Arctic skuas present on their territories were significantly lower among pairs with two chicks than among pairs with only one chick (Tables 4.2 and 4.4). This was true both for pairs which laid before the mean laying date and those that laid thereafter. However, at least among pairs which laid before the mean laying date, the trend was the same as in great skuas, ie the mean territorial attendance values and the percentage of adults present on their territories were lower among pairs with two chicks. During the post-fledging period Arctic skuas showed the same trends which were, however, statistically significant during this period (Tables 4.2 and 4.4).

In both species the differences in territorial attendance during the last two stages of the breeding season between pairs with different brood sizes seem to be due to pairs with broods of two being present together on their territories less often than pairs with broods of one (Tables 4.6 and 4.7). Among pairs which laid on or before the mean laying date, the percentage of occasions on which both adults were present on their territory was lower, but not significantly so, for pairs with two chicks than for pairs with one chick during the latter part of the pre-fledging period (Tables 4.6 and 4.7) These findings agree with the fact that among early-laying pairs of both species, the

mean territorial attendance values and the percentage of adults present on their territories were lower, although not markedly so, among pairs with two chicks than among pairs with one chick (Tables 4.2 to 4.5). Similarly, in agreement with the findings regarding mean territorial attendance values (Tables 4.2 and 4.3) and the percentage of adults present on their territories (Tables 4.4 and 4.5), the percentage of occasions on which both adults of early-laying pairs with two chicks were seen together was significantly lower than was the case for early-laying pairs with one chick, during the post-fledging period (Tables 4.6 and 4.7). The fact that the proportion of occasions on which both adults of a pair were seen together did not differ significantly between pairs with two chicks and pairs with one chick of either species, during the last two stages of the breeding season, when considering pairs which laid after the mean laying date, agrees with the results of other measures of attendance (Tables 4.2 to 4.5).

In the case of great skuas, the differences in territorial attendance between pairs with different brood sizes was also due in a large part to differing tendencies of pairs to leave their territories unattended. During the latter part of the pre-fledging period pairs of great skuas with two chicks were absent from their territory at the same time significantly more often than pairs with one chick (Table 4.9). This was true of pairs which laid before and after the mean laying date. During the post fledging period this difference was even

more marked, although the result was not statistically significant among pairs which layed after the mean laying date (Table 4.9) due perhaps to the small number of days of observation. Arctic skuas did not exhibit this pattern to any extent (Table 4.8).

3) Differences in territorial attendance between periods

In both species, pairs which which laid before the mean laying date and that subsequently had two chicks, showed a statistically significant increase in mean territorial attendance values and in the percentage of adults on their territories between the pre-laying period and the incubation period (Tables 4.2 to 4.5). This was also true of pairs of Arctic skuas which subsequently had only one chick, but not of great skuas which were to have broods of one. Pairs which laid after the mean laying date showed the same trends as equivalent pairs which laid earlier, apart from great skuas which hatched only one chick. In this case, they too showed an increase in attendance once they had laid their eggs (Tables 4.3 and 4.5). In fact only in this latter case was the increase in attendance between these two periods statistically significant among late-laying pairs (Table 4.5).

In all cases these differences in attendance between the pre-laying period and the incubation period were partly due to a significant decrease in the number of occasions on which both adults of a pair were absent at the same time (Tables 4.8 and 4.9). In addition pairs of Arctic skuas which laid before the mean laying date and that subsequently had either one or two chicks showed a statistically

significant increase in the proportion of occasions on which both adults of a pair were present at the same time between the pre-laying and the incubation period (Table 4.6). This same trend was apparent among Arctic skuas which laid after the mean laying date and which subsequently had broods of one (Table 4.6) and among early-laying pairs of great skuas which hatched two chicks (Table 4.7) and late-laying pairs of great skuas which hatched only one chick (Table 4.7).

Pairs of great and Arctic skuas with either brood size which laid before the mean laying date showed no significant differences between the incubation period and the early part of the pre-fledging period in any of the four measures of attendance (Tables 4.2 to 4.9). The general trend among early-laying pairs was of higher territorial attendance during the early part of the pre-fledging period in comparison with the incubation period (Tables 4.2 to 4.7).

However, in this respect pairs which laid after the mean laying date differed completely from pairs that laid earlier in the season. In terms of mean territorial attendance values, the percentage of adults present on their territories and the percentage of occasions on which both adults of a pair were present together, pairs of both species with either brood size showed a decrease in territorial attendance as soon as their chicks hatched (Tables 4.2 to 4.7). The decreases in the last two of these measures of attendance were statistically significant for pairs of great skuas with either brood size (Tables 4.5 and 4.7). Among Arctic skuas the decrease in the percentage of occasions on which both adults of a pair were seen

together was significant for pairs with two chicks (Table 4.6). The percentage of occasions on which both adults of a pair were absent at the same time did not differ significantly between the incubation period and the early part of the pre-fledging period for pairs of either species with either brood size which laid after the mean laying date (Tables 4.8 and 4.9).

When pairs which laid before the mean laying date were considered, in all but one case there was a significant decrease in mean territorial attendance values and in all cases a significant decrease in the percentage of adults on their territories between the early part and the later part of the pre-fledging period (Tables 4.2 to 4.5). The one exception to this decrease in the mean territorial attendance value between these periods was great skuas with one chick. However, given the significant decrease in the percentage of adults present on their territories between these two periods for this group of pairs and the fact that the mean territorial attendance values did actually decrease slightly, it seems reasonable to assume that this difference was genuine. The difference between these two periods in terms of the proportional decrease in mean territorial attendance values and the percentage of adults on their territories, was more marked among great skuas than among Arctic skuas.

Pairs which laid after the mean laying date showed exactly the same trends as were found among pairs which laid earlier in the season (Tables 4.2 to 4.5), although only significant in the case of the

percentage of adult great skuas present on their territories (Table 4.5).

These declines in territorial attendance between early and late pre-fledging periods were partly due to marked decreases in the percentage of occasions on which both adults were present together on their territory (Tables 4.6 and 4.7). These decreases were statistically significant in all cases except pairs of Arctic skuas which laid after the mean laying date (Table 4.6). Among Arctic skuas this would seem to be the only major factor in the decline in territorial attendance between these two periods since there were no significant increases in the percentge of occasions on which both adult of a pair were absent at the same time between these two periods (Table 4.8). In the case of great skuas, however, the percentage of occasions on which both adults were absent at the same time was significantly higher during the latter part of the pre-fledging period than during the earlier part for pairs of either brood size which laid after the mean laying date and for pairs with two chicks which laid before the mean laying date (Table 4.9). Pairs of great skuas with one chick which laid before the mean laying date showed the same trend, but the difference between periods was more marked among pairs with two chicks than among pairs with one chick.

Between the latter part of the pre-fledging period and the post-fledging period, pairs of Arctic skuas and pairs of great skuas which had two chicks and that had laid before the mean laying date showed significant decreases in mean territorial attendance values and the

percentage of adults present on their territories (Tables 4.2 to 4.5). This trend was also apparent among early-laying pairs of Arctic skuas with one chick (Tables 4.2 and 4.4) but not among early-laying pairs of great skuas with one chick (Tables 4.3 and 4.5) or among late-laying pairs of great skuas (Tables 4.3 and 4.5). The declines in the territorial attendance of Arctic skuas between these two periods were due to significant decreases in the proportion of occasions on which both adults of a pair were seen together on their territory (Table 4.6) and not by any increased tendency of adults to leave their territory unattended once their chicks had fledged (Table 4.8). In contrast, pairs of great skuas with either brood size which laid either before or after the mean laying date, did show an increased tendency to leave their territories unattended once their chicks had fledged. This trend was significant only among early-laying pairs (Table 4.9), and in combination with a significant decrease in the proportion of occasions on which both adults of early-laying pairs of great skuas with two chicks were present together on their territories (Table 4.7), resulted in significant decreases in the other two measures of attendance between these two periods (Tables 4.3 and 4.5). Early-laying pairs of great skuas with one chick and late-laying pairs of great skuas with either brood size showed an increased tendency to occur together on their territories during the post-fledging period compared to the latter part of the pre-fledging period (Table 4.7). This tendency was statistically significant among early-laying pairs

of great skuas with one chick but not among late-laying pairs.

4) Territorial attendance of great skuas in 1986

The sample sizes for 1986 (Table 4.10) were considerably lower than those for 1987. The results for 1986 agree with those for 1987 in that tests which gave non-significant results in the analysis of the 1987 data also gave non-significant results in the analysis of the 1986 data. However, in 1986 there was no significant difference between the mean territorial attendance values, during the early and late pre-fledging periods for pairs with two chicks. The non-significance of this result in the analysis of the 1986 data probably reflects the small sample sizes used in that year. Nonetheless in this case and in the decrease in attendance between early and late pre-fledging periods among pairs with one chick and the difference in attendance between pairs with different brood sizes during the latter part of the pre-fledging period, the data from 1986 do follow the same trends as in 1987 (Tables 4.3 and 4.10).

5) Territorial attendance of Arctic skuas in 1986

As was the case for great skuas ,the sample sizes for Arctic skuas in 1986 (Table 4.11) were smaller than those in 1987. Again the results for 1986 data agree with those for 1987 in that tests which were not significant in the analysis of the 1987 data were also not significant in the analysis of the 1986 data. However, the analysis of 1986 data did not indicate any significant differences between the mean territorial attendance values during the early and late part of the pre-fledging period for pairs of either brood size, or between the

mean territorial attendance values during the latter part of the pre-fledging period and post-fledging period for pairs with broods of two. Once again, however, the data did follow the same trends as in 1987 (Table 4.2 and 4.11).

6) Comparison of 1986 and 1987 data

As can be seen from Tables 4.12 and 4.13, the mean territorial attendance values of pairs with either brood size of either species did not differ significantly between 1986 and 1987 during any stage of the breeding cycle. The rather small sample of pairs studied in 1986 may be partly responsible for the non-significance of some of these results.

7) Comparison of 1986 and 1987 data with 1970s data

In all three comparisons between the mean territorial attendance values of pairs of great skuas which bred in 1976 and those which bred in 1986 and 1987 there was a very pronounced trend for attendance during the latter part of the pre-fledging period to be lower in the last two years (Table 4.14). This trend was statistically significant when pairs with two chicks were considered and when all pairs were considered but not among pairs with only one chick.

There were no significant differences in the attendance patterns of Arctic skuas which bred in 1979 and those which bred in 1986 or 1987 during the incubation period and the early part of the pre-fledging period. This was true for pairs with either brood size (Tables 4.15 and 4.16), although pairs with two chicks showed a trend towards lower

attendance in 1986 and 1987 during the early part of the pre-fledging period (Table 4.16). However, the proportion of occasions on which two adults were recorded on their territories during the latter part of the pre-fledging period was significantly lower in 1986 and 1987 than in 1979, for pairs with broods of either size (Tables 4.15 and 4.16).

8) The decision to leave territories unattended

Of the seventeen pairs of great skuas which left their territories unattended at least once during the latter part of the pre-fledging period in 1987, six pairs did so significantly less often than expected if birds left their territory at random with respect to the presence or absence of their mate (Table 4.17). The fact that all of the other eleven pairs exhibited this same trend (Table 4.17), although not statistically significant in any individual case, is significant in itself.

9) Breeding biology of skuas in 1987

The mean laying date of Arctic skuas in 1987 was the 25th of May. This did not differ from the mean laying dates in the late 1970s which were the 26th, 27th and the 24th of May in 1978, 1979 and 1980 respectively (Furness 1980). It would appear that the pairs of great skuas studied in 1987 laid later than was normal in the 1970s since the mean laying date in 1987 was the 21st of May compared to the 16th of May in the 1970s (Furness unpbl.).

The mean internal volume of great skua eggs which were laid in 1987 was significantly smaller than that of eggs laid in 1975 (Table 4.18). This was not the case for Arctic skuas (Table 4.18).

The proportion of pairs of both species of skua which laid one egg did not differ significantly between 1987 and the 1970s (Table 4.18).

Comparisons of the minimum and maximum hatching successes of Arctic skuas in 1987 and comparable data from the 1970s indicated that regardless of whether maximum or minimum values were studied, the proportion of skua eggs which hatched in 1987 and in 1979 did not differ significantly. The minimum hatching success of great skua eggs in 1987 did not differ significantly from the hatching success in 1975 (Table 4.18) although the maximum hatching success of great skua eggs in 1987 was significantly higher than that in 1975 (Table 4.18).

Both the maximum and the minimum fledging successes of great skuas in 1987 were significantly lower than in 1975 (Table 4.18). The maximum fledging success of Arctic skuas in 1987 was not significantly different from either the maximum or the minimum fledging success achieved by Arctic skuas in 1979 (Table 4.18). However, the minimum fledging success achieved by Arctic skuas in 1987 was significantly lower than the comparable figure for 1979 (Table 4.18). Further the minimum and maximum rates of post-fledging mortality among Arctic skua fledglings were significantly higher in 1987 than the comparable rates in 1979 (Table 4.18) as a result of which overall success of the Arctic skuas' breeding season in terms of the proportion of eggs laid which resulted in independent chicks at the end of the season was significantly lower in 1987 than in 1979 (Table 4.18).

The growth rate of Arctic skua chicks was significantly lower in 1987 than in 1979 since the observed distribution of 1987 data points above and below the logistic growth curve of Arctic skua chicks reared in 1979 (Furness 1980) differed significantly from expectations (Table 4.19, Fig 4.1). This was also true for chicks of great skuas (Table 4.19, Fig 4.2). However, when the data were split into three age classes; 0-16 days old, 17-32 days old and 33-49 days old, only during the first two stages did the observed distribution of great skua chick weights in 1987 differ significantly from expectations (Table 4.19, Fig 4.2). During the last stage of the pre-fledging period when the growth curve reached its asymptote, the great skua chicks in 1987 were as heavy for their age as would be expected since the distribution of data points above and below the logistic growth curve of chicks growing "typically" in 1975 did not differ significantly from expectations (Table 4.19, Fig 4.2).

10) Seabird population changes on Foula between 1976 and 1987

The results of the census in 1987 and of a similar survey carried out in 1976 are presented in Table 4.20. These figures show that the population of every species of seabird which is commonly victimised by skuas, with the exception of the gannet (Sula bassana), is now considerably lower than in 1976. Re-analysis of these data indicated that the numbers of individuals of the main host species returning with fish, and hence available to be chased, have declined by approximately thirty five percent for both species of skua. This is a conservative estimate as it assumes that breeding success, and

consequently the proportion of the host populations returning with fish to their chicks, has not decreased along with the decline in population sizes.

Discussion

The two factors which are intuitively of overriding concern in determining the amount of time which birds must devote to foraging in preference to other activities, are food requirements and food availability.

At times when individuals only have to feed themselves it is likely that the food requirements and hence the amount of time spent foraging will vary little between individuals of the same age, sex and species. This is liable to be the case at least during the non-breeding season, and the results of the present study indicate that this was also the case during the early stages of the breeding season since pairs which subsequently had broods of one and two, did not differ significantly in any aspect of territorial attendance during the pre-laying and incubation periods when they only had to feed themselves (Tables 4.2 to 4.9).

However, when breeding birds have chicks to feed it is intuitive that the food requirements of individuals should differ depending on the number of offspring which they attempt to rear. It would be expected that the higher the number of chicks to be fed, the more time adults would have to spend foraging to collect enough food to meet their demands. Two recent studies in which the food demands placed on

adult birds were experimentally increased, either by replacing fed chicks with hungry chicks and removing food delivered by adults (Masman et al. 1988b), or simply by increasing the brood size (Reid 1987), resulted in the parent birds devoting more time to foraging. In this respect the results of the present study are counter-intuitive in that, with the exception of late-laying pairs of great skuas, the territorial attendance of pairs with two chicks did not differ significantly in any respect from pairs with one chick during the early part of the pre-fledging period (Tables 4.2 to 4.9). Although the differences were in the expected direction in most cases (ie pairs with two chicks were present on their territories less often than pairs with one chick); these results imply that the food demands of two small chicks are little higher than those of one small chick and that adults can meet the food requirements of the former with little extra effort over and above that required to feed the latter. Furness (1980) found similar trends among Arctic skuas in the 1970s, and Furness (1977) found that even great skuas whose brood size had been experimentally increased to three or four chicks did not spend significantly more time foraging during the early part of the pre-fledging period than pairs with broods of one or two. During either the latter part of the pre-fledging period when chicks grew rapidly to fledging weight and hence required a lot of food, or else during the post-fledging period when chicks were large, pairs of great skuas and pairs of Arctic skuas with two chicks to feed had, as expected,

significantly lower territorial attendance scores either in terms of mean territorial attendance values or the percentage of adults present on their territories than did pairs with one chick (Tables 4.2 to 4.5). In most of the cases which were not statistically significant the differences in attendance between pairs with different brood sizes followed this same trend. It would therefore appear that contrary to the results of Reid (1987), pairs with two chicks had to forage significantly more than pairs with one chick only when the chicks were large and required a lot of food.

These differences in attendance scores during the latter part of the pre-fledging period and the post-fledging period, between pairs with two chicks and pairs with one chick, were more marked among great skuas than among Arctic skuas when the differences were expressed as percentages of the attendance scores of pairs with one chick. The reason for this difference between the species is that the extent to which pairs with two chicks were present together on their territories less often than pairs with one chick, was if anything greater among great skuas than among Arctic skuas (Tables 4.6 and 4.7). In addition while pairs of great skuas with two chicks were absent from their territories at the same time significantly more often than pairs with one chick, during the last two stages of the breeding cycle (Table 4.9), this was not the case for Arctic skuas (Table 4.8). It would appear that two chicks were relatively more of a "strain" than one chick on great skuas than on Arctic skuas.

Of equal importance to the food requirements and hence foraging effort of breeding skuas is whether or not they have chicks to feed at all and how large these chicks are. It might be expected that as soon as chicks hatch, breeding adults would have to forage either more frequently or else for longer periods at a time in order to meet the food demands of their chicks as well as their own. The fact that among pairs of both species with either brood size which laid before the mean laying date, there were no significant decreases in either mean territorial attendance values (Tables 4.2 and 4.3) or the percentage of adults present on their territories (Tables 4.4 and 4.5) between the incubation period and the early part of the pre-fledging period implies that, contrary to expectations, one or even two small chicks required little or no extra foraging effort on the part of the adults. That this was not always the case among pairs which laid after the mean laying date (Tables 4.2 to 4.5), points to the importance of food availability to skua foraging effort (see below). The former results almost certainly reflect the fact that the rate of weight gain by skua chicks follows a logistic curve. During the first few days after hatching when skua chicks gain weight relatively slowly, their food demands are relatively low such that, provided food availability is high, the adults can meet their food requirements with little extra effort.

However, the subsequent rapid rate of growth of skua chicks which must entail high food requirements (Furness 1977) resulted in pronounced reductions in mean territorial attendance values and the

percentage of adults present on their territories between the early and later parts of the pre-fledging period among pairs of both species of skua with either brood size (Tables 4.2 to 4.5). There were no exceptions to this trend, and those differences which were not statistically significant were almost all due to small sample sizes. Clearly one or two large chicks required greater foraging effort by parent birds than one or two small chicks respectively. The fact that, on the whole these declines in territorial attendance were more marked among pairs with two chicks than among pairs with one chick implies that two large chicks represented more of a "strain" relative to two small chicks than did one large chick relative to one small chick. Since these differences were more marked among great skuas than among Arctic skuas it appears that large chicks were relatively more of a "strain" in comparison with small chicks to great skuas than to Arctic skuas.

The declines in territorial attendance between these two periods were partly due to declines in the proportion of occasions on which both adults of a pair were seen together on their territories (Tables 4.6 and 4.7). This was true for both great and Arctic skuas, although the differences were not statistically significant among Arctic skuas which laid after the mean laying date. However, unlike Arctic skuas, great skuas also showed marked increases, which were statistically significant in all cases except early-laying pairs with one chick, in the percentage of occasions on which territories were left unattended

between early and late pre-fledging periods (Table 4.9). This explains why the reductions in mean territorial attendance values and the percentage of adults present on their territories between these two periods were more marked among great skuas than among Arctic skuas.

Furness (1977) stated that the food requirements of great skua chicks peak at around 35 days of age and then fall slightly thereafter as growth rate declines and the chicks fledge. It might be expected that foraging effort of adults would decrease once chicks fledge and territorial attendance scores would increase between the latter stage of the pre-fledging period and the post-fledging period. In no case was this observed in the present study; the mean territorial attendance values and the percentage of adults present on their territories were always lower during the post-fledging period than the latter part of the pre-fledging period (Tables 4.2 to 4.5). This trend was not statistically significant in all instances (particularly among late-laying pairs where sample sizes were small), but was noticeably more marked among pairs with two chicks than pairs with one chick. Again these results imply that, two large chicks were more of a "strain" on adults relative to two smaller chicks than was one large chick relative to one smaller chick. This would appear to have been true more for great skuas than for Arctic skuas since pairs of great skuas with one chick showed declines in attendance similar to those of Arctic skuas with one chick while the declines in attendance of pairs of great skuas with two chicks were much more marked than among pairs of Arctic skuas with two chicks.

The reasons for these further declines in territorial attendance between the latter part of the pre-fledging period and the post-fledging period differ between Arctic skuas and great skuas which laid before the mean laying date. While pairs of great skuas with either brood size showed a significant increase in the percentage of occasions on which both adults of a pair were absent at the same time, between these two periods (Table 4.9), pairs of Arctic skuas with either brood size did not (Table 4.8). In addition the declines in the percentages of occasions on which both adults of a pair were present together on their territory were more marked among Arctic skuas than great skuas.

If the food requirements of skua chicks are maximal before they fledge, and decline thereafter, the universal trend for adult skuas to have lower attendance scores and hence to forage more during the post-fledging period before their chicks became independent cannot be explained by increased food requirements. In the mid 1970s a detailed study of the diet of great skuas was carried out (Furness 1977, Furness and Hislop 1981). The diet of great skuas can be divided into three main categories; sandeels (Ammodytes marinus), whitefish and "other" items which include; mammals, birds, bird eggs, invertebrates and berries. The proportions of these different food types present in the diet of non-breeding great skuas were found to vary through the course of the season; items of food belonging to the "other" category were more common early and late in the season,

particularly in 1976 (Furness 1977, Furness and Hislop 1981). The fact that adult seabirds are available as prey throughout the breeding season, as presumably are barnacles (Lepas sp) and mussels (Mytilus edulis), yet only appear in the diet to any noticeable extent early and late in the breeding season, was taken to indicate that these food items are less profitable energetically than sandeels or whitefish and only occur in the diet when availability of these other food items is low. This would indicate that food availability is low early and late in the breeding season (Furness 1977, Furness and Hislop 1981).

Thus the increased amount of time spent foraging by adult skuas once their chicks had fledged may well reflect lower food availability late in the season, such that with large, if not rapidly growing, chicks to feed during the post-fledging period, greater foraging effort was required to meet their demands.

Not only will decreased food availability late in the season require greater foraging effort on the part of the members of each pair as the season progresses, but pairs of skuas which lay late in the breeding season might be expected to have more difficulty in feeding their chicks than pairs which lay earlier. This idea was suggested in relation to great skuas by Furness and Hislop (1981) but it is also likely that as the chicks of other species of seabird fledge, late-laying pairs of Arctic skuas will have increasing difficulty in obtaining sufficient food for their chicks as the number of potential hosts carrying fish to their chicks, and hence available to be chased, declines late in the season. These predictions are supported by the

observation that during both the early and the later part of the pre-fledging period, pairs of great skuas and Arctic skuas which laid after the mean laying date had lower (although not always significantly so) mean territorial attendance values than pairs with the same brood size which laid earlier (Table 4.1) and also lower values for the percentage of adults present on their territories (Tables 4.4 and 4.5) and the percentage of occasions on which both adults of a pair were present together (Tables 4.6 and 4.7). Similarly members of pairs of great skuas which laid after the mean laying date were absent from their territories at the same time more often than pairs which laid earlier in the season during both the latter part of the pre-fledging period and the post fledging period (Table 4.9). In addition, while pairs of skuas which laid before the mean laying date almost all showed an increase in mean territorial attendance values and the percentage of adults present on their territories between the incubation period and the early part of the pre-fledging period (Tables 4.2 to 4.5), this was never the case for late-laying pairs. As soon as the chicks of late-laying pairs hatched, the territorial attendance in terms of mean territorial attendance values and the percentage of adults present on their territories declined (Tables 4.2 to 4.5). In the case of the latter measure of attendance, these declines were actually statistically significant among all pairs except Arctic skuas with one chick.

All of these trends are in agreement with the prediction that late-laying pairs of skuas would have increased difficulty in meeting the food requirements of their chicks due to reduced food availability late in the season.

Furness (1977) found that in 1976, there was a significant positive correlation between the percentage of sandeels in the diet of great skuas and the amount of time breeding adults spent on their territories. He concluded that since sandeels were the only prey item in the diet which produced this result, that sandeels were the preferred diet of great skuas. Furness (1977) also found that the percentage of great skuas present on selected territories during spot observations was lower on most days in 1975 than in 1976. He suggested that this was related to differences between the two years in the availability of Norway pout (Trisopterus esmarkii), haddock (Melanogrammus aeglefinus) and whiting (Merlangius marlangus) relative to that of sandeels.

Since there were no significant differences between the mean territorial attendance values of skuas studied in 1986 and those studied in 1987 (Tables 4.12 and 4.13) it would seem that food availability did not change to any great extent between these two years.

During the early stages of the 1986 and 1987 breeding seasons, Arctic skuas appear to have fared as well as in 1979 in that mean laying date, mean clutch size, mean egg volume, hatching success and territorial attendance during the incubation period did not differ

significantly between the last two years and 1979 (Tables 4.15, 4.16 and 4.18). The situation as regards great skuas is not so clear. The mean laying date of the pairs of great skuas studied in 1987 was five days later than in the past and the mean egg volume in 1987 was significantly lower than in 1975 (Table 4.18). This might indicate that environmental conditions early in the season were not as favourable to great skuas in 1987 as in 1975. However, the mean clutch size and hatching success of great skuas in 1987 was as good as, or better than, in 1975 (Table 4.18). Work carried out by Hamer on Foula in 1988 (Hamer in prep.) indicated that even in a season in which breeding failure of great skuas was almost complete, the adults themselves were as heavy and presumably in as good body condition during the incubation period as were adults which bred in the mid-1970s. Therefore, even when great skuas are considered, there is no clear evidence that conditions during the early part of the breeding season have been any worse in recent years than in the mid-1970s.

However, the territorial attendance of skuas during the latter part of the pre-fledging period was lower in 1986 and 1987 than in the mid-to-late 1970s (Tables 4.14-4.16). These differences were statistically significant in all cases except for the comparison between the attendance of pairs of great skuas with one chick. Eight out of the nine pairs of great skuas with one chick which were studied in 1986-87 did actually have lower mean territorial attendance scores than the pairs studied in 1976. Thus even among pairs of great skuas with one

chick, the trend for poorer attendance during this period of the breeding season in the last two years compared to the situation in 1976 is apparent.

These results indicate that breeding skuas had to spend a considerably higher proportion of each day foraging in 1986-87 than in the 1970s in order to meet their chicks food requirements. Clearly these results indicate that food availability to skuas was lower in 1986 and 1987 than in the mid-to-late 1970s. The skuas' response to this situation has obviously been to increase their foraging effort in an attempt to maintain chick growth rates. The fact that the growth rates of skua chicks in 1987 were significantly lower than in the mid-to-late 1970s (Table 4.19, Figs 4.1 and 4.2) indicates that in spite of this extra effort on the part of the parents, they were not collecting food as rapidly as required to maintain these previously high rates of growth. Again great skuas and Arctic skuas differ in the reasons underlying these changes in attendance between years. Furness (1980) does not seem to have recorded any occasions on which both adults of a pair of Arctic skuas were absent from their territory at the same time. This was also an extremely rare occurrence in 1986 and 1987 and was recorded on only five occasions during the whole of the pre-fledging period. Thus Arctic skuas do not appear to have been leaving their territories unattended any more often in 1986-87 than in 1979. Indeed, the significantly lower attendance of Arctic skuas in 1986-87 was due purely to a reduction in the proportion of occasions on which both adults of a pair were seen together (Tables 4.15 and 4.16).

Furness and Hislop (1981) do not present the data from which they derived mean territorial attendance values. Nonetheless, they state that pairs of great skuas with one or two chicks never left their territories unattended. In 1986 and 1987 this occurred frequently even before the chicks had fledged. Thus, unlike Arctic skuas the decline in the attendance of great skuas during the latter part of the pre-fledging period between 1976 and 1986-87 was due to an increased tendency of the adults to leave their territories unattended.

That this tendency was involuntary and atypical behaviour for great skuas is evinced by the fact that great skuas never left their territories unattended in 1976 and some pairs which bred in 1986 and 1987 did not do so either. Also, of those seventeen pairs which did leave their territories unattended at least once, six pairs did so significantly less often than would be expected if leaving the territory unattended was not undesirable, and the attendance of the other eleven pairs followed the same pattern (Table 4.17). This difference between the species had important repercussions for the fledging success which they achieved.

Although the estimated minimum fledging success of Arctic skuas in 1987 was significantly lower than the equivalent value in 1979, the fact that the estimated maximum fledging success of Arctic skuas in 1987 did not differ significantly from either the estimated maximum or estimated minimum fledging success of Arctic skuas in 1979 (Table 4.18), means that there is no conclusive proof that the fledging

success of Arctic skuas in 1987 was any worse than in 1979. Furness (1977) found that there was a large variation in the intensity of predation on birds by great skuas between years. He also found that there were differences between years in the predation intensity on different species; in years of high bird predation there was a higher proportion of great skua chicks killed than in years of low predation. Furness (1977) suggested that years in which food is scarce result in greater bird predation by great skuas, and with increasing scarcity of food, there is a "proportionately greater tendency for great skua chicks to be taken". The reason for this is that when food is readily available, predation of chicks is prevented by the protection of the non-foraging parent. However, under the conditions of food scarcity prevalent in 1986 and 1987, pairs of great skuas had to forage for such a high proportion of the day that they frequently left their territories and hence chicks unprotected. Consequently the level of predation on great skua chicks was high and the fledging success of great skuas was significantly lower in 1987 than in 1975 (Table 4.18).

Barrett and Runde (1980) found that under conditions of food shortage, kittiwakes (Rissa tridactyla) in Norway, like great skuas on Foula in 1986 and 1987, had abnormally low adult attendance at nests with chicks. As has been suggested in this study, Barrett and Runde (1980) suggested that during periods of food scarcity, adults sacrifice constant protection of chicks in order to increase their chick-feeding capacity. As was the case among great skuas, this behaviour exposed the kittiwake chicks to high risks of predation,

although in their case the direct effect of the food shortage was through chick-starvation rather than predation (Barrett and Runde 1980). Clearly the manner in which reduced food availability acts, differs between species. This point is further exemplified by the ultimate fate of Arctic skua chicks on Foula in 1987.

The level of predation on Arctic skua fledglings by great skuas on Foula varies widely between years (Furness 1977,1987a). Furness (1977,1987a) suggested that the level of predation on Arctic skua fledglings depends on the availability of fish to great skuas during the weeks when Arctic skua chicks begin to fledge and also on the spatial distribution of the territories of the two species. When many Arctic skua territories are adjacent to those of great skuas, the fledgling Arctic skuas cannot make their initial practice flights without straying over the territories of great skuas. If the latter are short of food they would obviously find fledgling Arctic skuas a valuable supplementary food source, which could save time spent foraging at sea (Furness 1977). In 1986 and 1987 great skuas were obviously short of food (as witnessed by their habit of leaving chicks unprotected) and the present day distribution of the two species of skua on the island of Foula (Furness 1987a Fig 98) is such that practically all Arctic skua territories are very near to those of great skuas. Consequently, although breeding Arctic skuas did not seem to be suffering directly from reduced food availability to the same extent as great skuas and managed a maximum estimated fledging success

comparable to that in 1979, the vast majority (at least 82%) of fledged chicks were killed by great skuas. Thus the breeding success of Arctic skuas in 1987 (measured as the proportion of eggs laid which resulted in independent young leaving the island) was significantly lower in 1987 than in 1979 (Table 4.18). While the reduced food availability had a direct detrimental effect on great skuas, only through the indirect action of great skuas was the breeding success of Arctic skuas drastically reduced.

It is felt that the territorial attendance of birds which forage at a distance from their nest site may actually be one of the most sensitive indicators of changes in food availability. Where food availability declines only slightly between years, adults may be able to deliver food to their chicks at a high enough rate to maintain chick-growth-rates and fledging success, in the year of poorer food availability, at the level of the previous year. If only these aspects of breeding biology were studied, no indication of environmental changes would be detected. However, it is likely that even under conditions of slightly reduced food availability, adults could only achieve this status quo by increasing their foraging effort. Hence territorial attendance may be the first sign, among breeding birds, of food shortage. The fact that the breeding success of skuas in 1987 was much reduced in comparison with the mid to late 1970s is a reflection of the severity of the food shortage. The question which remains is what is the reason for this decline in food availability?

Over the last few years there has been increasing concern over the complete breeding failure of Arctic terns (Sterna paradisaea) in Shetland. Recent studies (Monaghan et al. 1988) have suggested that these breeding failures were due to a shortage of sandeels of the particular size with which Arctic terns preferentially feed their chicks. These results seem to indicate that there has been a marked decrease in the availabilty of sandeels around Shetland. Clearly this reduced availability of sandeels has had severe consequences for skuas as well as terns in Shetland. The close agreement between the results of the present study and the ongoing comparison between the breeding biology of a population of Arctic terns which is suffering from reduced food availability (those breeding in Shetland) and one which is not (those breeding on Coquet Island) (Monaghan et al. 1988) is gratifying. Just as was true of skuas, particularly Arctic skuas, the egg volume, clutch size and hatching success of Arctic terns breeding under the two different environmental conditions were not significantly different. However, the Arctic terns in Shetland foraged more than their counterparts to whom food was more readily available, and frequently left their chicks unattended. In spite of increased parental foraging effort, the growth rates of Arctic tern chicks were significantly slower on Shetland and the fledging success was lower here than on Coquet Island due to chick starvation and predation of unguarded chicks by, in this case, common gulls (Larus canus) (Monaghan et al. 1988). The similarities between this pattern and that found among great skuas is remarkable. This decline in sandeel

availability is certain to have had effects on the feeding success of other seabird species including puffins (Fratercula arctica), guillemots (Uria aalge), razorbills (Alca torda) and kittiwakes, all of which are host species of great skuas and Arctic skuas. Such a food shortage may have resulted in the host species feeding their chicks on smaller fish than "normal" (as is true of Arctic terns (Monaghan et al. 1988)), in victims being less willing to part with their fish to maurauding skuas or, perhaps more seriously, in an overall reduction in the number of individuals of the host species returning with fish. This last change may come about either because, for a given breeding population, the proportion of birds finding fish decreases or because the actual breeding population decreases. All of these possibilities would result in kleptoparasitically feeding skuas having to forage for longer periods of time each day in order to collect the quantity of fish they require to meet their own, and their chicks', energy demands.

The census data presented in Table 4.20 clearly indicate that on Foula, the populations of all the main host species of skuas have declined markedly since the mid-1970s, as a consequence of which skuas have at least 35% fewer potential hosts to chase. On top of this, the results in chapter 2 indicate that the victims of skuas were less willing to part with their fish to attacking skuas and hence, at least against puffins, skuas were significantly less successful in stealing fish than in the mid-to-late 1970s.

Since Arctic skuas feed almost exclusively by kleptoparasitism during the breeding season in Shetland (Furness 1978a, 1980) it is reasonable to conclude that, at least in their case, the decline in territorial attendance during the latter part of the pre-fledging period between 1979 and 1986 and 1987, was due to a marked decrease in the availability of fish carrying hosts and lower success rates in stealing fish.

Furness (1977) calculated that the total food intake from kleptoparasitism by great skuas on Foula could only represent 5% of the total energy demand of the population, and concluded that kleptoparasitism is only a minor feeding technique of great skuas. Since the ability of Arctic skuas to rear their chicks seems to have been affected less by the reduction in food availability than that of great skuas which were forced to leave their chicks unguarded and hence open to predation by neighbouring skuas, during the latter part of the pre-fledging period, it is possible that the reduction in the profitability of kleptoparasitism has been less under these conditions than the reduction in the profitability of attempting to catch fish directly. This situation could have arisen because the host species of kleptoparasitic skuas, foraged more than normal to compensate for the food shortage in an attempt to maintain the rate of growth of their chicks. In so doing the host species could have maintained a relatively high level of food availability to the kleptoparasitic skuas compared to the actual availability of fish in the sea which non-kleptoparasitic skuas that attempted to catch fish for themselves

would have encountered. That this is a plausible argument is supported by the fact that Arctic terns in Shetland made significantly more foraging trips per day in 1987 than Arctic terns breeding on Coquet Island (Monaghan et al. 1988).

If this was the case, then should the food shortage continue, great skuas might be expected to become increasingly predatory and kleptoparasitic. In this event, the consequences could be severe both for the host species and for Arctic skuas. Grant (1971) found that late in the season, as the ratio between the number of skuas to puffins declined, the probability of a puffin retaining its fish declined. It is likely, therefore that the host species would suffer because of the increased pressure exerted by the larger number of skuas actively seeking victims. Arctic skuas would suffer from increased competition for depleted food sources from large numbers of great skuas. This could lead to Arctic skuas leaving their chicks unguarded while both parents forage at the same time, and consequently a reduction in their fledging success.

Even if great skuas do become more kleptoparasitic in response to continued food shortage, competition with Arctic skuas for a reduced number of hosts which may become less willing to part with their food, may reduce the potential profitability to great skuas of feeding in this way. Thus, regardless of whether great skuas become more kleptoparasitic or not, their territorial attendance might be expected to decline even earlier and further during the chick-rearing period if

the reduced availability of sandeels continues. The fact that the attendance of late-laying pairs of great skuas, which presumably suffered from even lower food availability than early-laying pairs (Furness and Hislop 1981), declined as soon as their chicks hatched and subsequently declined even further than pairs which layed earlier, probably indicates the trend which all pairs will show in the future. In this situation great skua predation of great skua chicks and Arctic skua fledglings is likely to remain high or even increase as both species leave their chicks unguarded more often. Thus, even if chicks do not starve then predation may result in continued or worsening breeding failure of both species of skua.

Chapter 5

Theory of Flight.

Introduction

The ability to fly has imposed severe constraints on the morphology of all animals which have this capability. As a result members of the Class Aves are extremely conservative in their morphology in comparison with members of other vertebrate classes such as the Class Mammalia. One of the most obvious constraints that the ability to fly has imposed on birds is in the maximum weight which they can attain while retaining the power of flight. The largest extant flying birds, for example whooper swans (Cygnus cygnus), which weigh about 12kg are approximately 6000 times heavier than the smallest hummingbirds (Family Trochilidae) which weigh about 2g. However, the largest terrestrial mammals, African elephants (Loxodonta africana) which weigh about 7000kg are approximately 1,000,000 times heavier than common shrews (Sorex araneus).

Nonetheless, there is among birds a considerable diversity in overall morphology with each species having become, through the process of natural selection, adapted to its own lifestyle. Many of the morphological differences which exist between species of bird can be attributed to adaptations to the use of particular specialised feeding techniques. The actual feeding apparatus, including the bill, is one of the most variable structures in avian anatomy and has consequently been the subject of much research into morphological adaptations to feeding techniques (Bowman 1961, references in Bock

1974). Two of many possible examples of birds with highly specialised feeding techniques which possess highly peculiar bills adapted to the use of that feeding technique are crossbills (Order Passeriformes Family Fringillidae) which feed on pine cones, and flamingoes (Order Ciconiiformes Family Phoenicopteridae) which feed by filtering micro-organisms from water. In many species of bird, the feeding technique which they employ requires not only a particular bill morphology but also a particular wing morphology. One of the best examples of this is the hummingbirds whose bones of the forearm are considerably shorter than in most other birds while the hand-wing bones are much elongated. This has resulted in wings which consist mostly of the manus. In addition, the joints of the wing skeleton, with the exception of the shoulder joint, are practically rigid (Welty 1964). These adaptations are beneficial to their feeding technique which involves prolonged hovering while drinking nectar from flowers. Many other species of bird possess a wing and body morphology which is adapted to their method of feeding, although few have gone to such extremes as the hummingbirds.

As has been mentioned in previous chapters, it has been suggested (Brockman and Barnard 1979) that kleptoparasites can be divided into so-called "specialists" and "opportunists". Brockman and Barnard (1979) state that the ability to be agile in the air may facilitate the evolution of kleptoparasitism by a species. They also state that frigatebirds, as specialist kleptoparasites possess morphological

features which enhance their aerobatic flight and hence represent pre-adaptations which are responsible, at least in part, for their reputation as kleptoparasites. They cite the small unwebbed feet, the vestigial uropygial gland and the extremely large wingspan relative to body weight as adaptations for aerobatic flight. Barnard (1985) states that the unique morphology of frigatebirds is the result of adaptations specifically to enhance kleptoparasitic performance. Brockman and Barnard (1979) also include skuas in the "specialist" kleptoparasite group and state that they too are built for sustained and manoeuvrable flight. They do not present any evidence to suppport this statement. In addition to agility it is likely that in order for a kleptoparasite to be successful on a regular basis that it should be able to fly faster than its victim and be able to accelerate rapidly.

The hypothesis which the morphological study in the following chapter was carried out to test is that the morphology of skuas, as "specialist" kleptoparasites, differs from that of their close relatives, the "opportunistically" kleptoparasitic gulls, in ways which mean that they are; more agile, able to fly faster and to accelerate more rapidly than gulls and hence that the evolution of "specialised" kleptoparasitic behaviour either requires or has resulted in particular morphological adaptations. In order to test this hypothesis, it is first of all necessary to determine the morphological features which would represent such adaptations and therefore to understand the ways in which the aerodynamic properties

of a bird vary in accordance with the shape and size of its body and wings. Thus a summary of the basic principles of the theory of flight is presented.

The outline of the theory of flight which is presented in this chapter is based on the theory of animal flight developed by Pennycuick (1968b,1969,1975), rather than on the vortex theory of animal flight proposed by Rayner (1979). These two theories differ in the way in which profile power scales with speed and in particular in the way in which induced power is calculated. However, both theories indicate that induced power decays, at least at high speeds, as V^{-1} such that induced power is negligible at high speeds. Rayner (1979) proposed that profile power increases with V and as V^3 at high speeds, while Pennycuick (1975) proposed that profile power is independent of speed. Pennycuick (1968b) did show that at high speeds, profile power increased with speed, so once again the two theories do agree in general, at least at high speeds. Since this study is concerned particularly with high speed performance and the two theories do seem to agree in their major conclusions on how power required scales with speed, at least at high speeds, it was decided, for the sake of simplicity, to refer to the quasi-steady-state analysis of Pennycuick (1975). As this chapter is essentially a summary of pre-existing theories its contents are, for the sake of clarity, drawn to a large extent directly from previous publications, particularly Pennycuick (1975).

The theory of flight

1) Calculation of the power required to fly

Bird flight can be divided into three main categories:

a) Powered flapping flight.

b) Gliding flight.

c) Soaring flight.

Since kleptoparasitic chases typically involve high speed flapping flight, only powered flapping flight is considered in this summary.

In order to maintain steady horizontal flight birds must generate an upward force (lift) to counteract the effects of gravity and a propulsive force (thrust) to counteract the backward force (drag) generated by the movement of their solid form through the air. In order to produce these forces flying animals must generate power. In birds the power required to fly is generated mainly by the pectoral muscles which are located within the main body of the bird. According to classical aerodynamic theory the total mechanical power required to fly can be divided into various components. In the case of a flying animal these are as follows:

a) Induced power - the power required to support the weight of the bird in the air.

b) Parasite power - the power required to overcome the skin friction and form drag of the body.

c) Profile power - the power required to overcome the profile drag of the wings.

d) Inertial power - the power required to accelerate the wings at each stroke.

e) Basal Metabolism - the power required to maintain homeostasis at thermoneutrality.

f) Circulation and Respiration power - the power required to pump the blood and ventilate the lungs.

Each of these components is considered in turn below.

a) Induced Power

In horizontal flight the upward reaction on the wings must equal the weight of the bird and this implies that the rate at which downward momentum is imparted to the air is numerically equal to the weight. This rate of change of momentum is the product of a downward induced velocity (Vi) and the mass of air to which this velocity is imparted in unit time, which in turn depends on the induced velocity (Vi), the air density (p) and the disc area (Sd). In the case of a bird which is hovering, for example a hummingbird, the bird's body remains stationary (forward speed V = 0) and the wings beat back and forth almost horizontally, the wingtips describing a figure of '8' while sweeping out an area known as the disc area (Pennycuick 1968b figure 7). This consists of two semi-circles about the shoulder joints, joined together across the body and defined by the equation

$$Sd = \pi b^2/4, \qquad (5.1)$$

where b is the wingspan. The term "induced velocity" refers to the velocity with which air passes through the wing disc. The air reaches this velocity as a result of accelerating downwards into an area of

reduced pressure above the wing disc. Because there is a similar pressure gradient below the bird, the air continues to accelerate downwards after passing through the wing disc and eventually reaches a velocity of 2Vi far below the bird. The mass flow (fm) through the wing disc in hovering, when V= 0, is given by the equation

$$fm = Sd.Vi.p. \tag{5.2}$$

The air is eventually accelerated to 2Vi , so the rate of change of momentum which equals the weight (W) is

$$fm.2Vi = W = 2.Sd.Vi^2.p, \tag{5.3}$$

so that

$$Vi = W^{1/2}/(2.Sd.p)^{1/2}. \tag{5.4}$$

The induced power in hovering (Pih) is

$$Pih = W.Vi = W^{3/2}/(2.Sd.p)^{1/2}. \tag{5.5}$$

In forward flight when V > 0, the mass flow through the wing disc is the product of the air density, the disc area and the resultant of the induced velocity and the forward speed. The faster a bird goes, the greater is the mass of air which passes through the wing disc in unit time, hence the less induced velocity is needed to produce the required rate of change of momentum to balance the weight. At a forward speed V the mass flow is

$$fm = p.Sd.(V^2 + Vi^2)^{1/2}. \tag{5.6}$$

When Vi is small compared to V, as is the case in fast flight, this equates to

$$fm = p.Sd.V, \tag{5.7}$$

so that the rate of change of momentum is

$$2.Vi.fm = W = 2.Vi.p.Sd.V, \quad (5.8)$$

so that

$$Vi = W/(2.p.Sd.V). \quad (5.9)$$

The induced power in forward flight (Pi) is still the product of the weight and the induced velocity, so

$$Pi = W.Vi = W^2/(2.p.Sd.V). \quad (5.10)$$

b) Parasite power

This component of the power required to fly is needed to overcome the parasite drag created at all flying speeds by the body of the bird which, no matter how streamlined, creates some drag by virtue of its sheer bulk. Parasite power (Ppar) is given by the equation

$$Ppar = 1/2.p.V^3.A, \quad (5.11)$$

where A is the equivalent flat plate area of the body, which is itself given by the equation

$$A = Sb.CDpa, \quad (5.12)$$

where Sb is the actual cross-sectional area of the body at its widest point and CDpa is the parasite drag coefficient. The equivalent flat plate area of a bird is a measure of how streamlined it is. It is very difficult to measure Sb accurately on corpses, and since the specimens which were available to be measured in this study had all been frozen, the shapes of their bodies were distorted in any case. Thus it was decided not to measure the cross-sectional areas of the bodies of the specimens studied. Pennycuick et al.(1988) have presented a technique for determining the value of A solely on the basis of the mass of the

specimen, but since the aim of this study was to determine whether skuas differ in their morphology from equivalently sized gulls their seemed to be little point in determining a value for A based purely on their mass. Hence no further details are presented on the methods of calculation outlined in Pennycuick et al.(1988).

The sum of the induced and parasite powers is the power required to fly by a bird consisting of a streamlined body supported by an ideal actuator disc, the work needed to flap the wings to and fro being neglected. This may be regarded as an ideal bird. The curve of power required versus forward speed for such a bird is illustrated in figure 2 of Pennycuick (1975). This curve is "U" shaped with a minimum at the minimum power speed (Vmp), at which the power required to fly is at an absolute minimum denoted (Pam). At a somewhat higher speed, denoted Vmr, which is defined as the point of contact between the power curve and a tangent to the curve which is drawn from the origin, the ratio of power required to speed achieved is a minimum. At this speed the distance travelled per unit work done is a maximum. This is the maximum range speed at which the power required to fly is denoted Pmr.

Expressions for Vmp, Pam, Vmr and Pmr were derived by Pennycuick (1975) and are as follows;

$$Vmp = \frac{0.760.k^{1/4}.W^{1/2}}{p^{1/2}.A^{1/4}.Sd^{1/4}}, \qquad (5.13)$$

$$Pam = \frac{0.877.k^{3/4}.W^{3/2}.A^{1/4}}{p^{1/2}.Sd^{3/4}}, \qquad (5.14)$$

$$Vmr = \frac{k^{1/4}.W^{1/2}}{p^{1/2}.A^{1/4}.Sd^{1/4}}, \quad (5.15)$$

$$Pmr = \frac{k^{3/4}.W^{3/2}.A^{1/4}}{p^{1/2}.Sd^{3/4}}, \quad (5.16)$$

where k is the induced power factor with value 1.2.

c) Profile power

The third major component of the power required to fly is that which is required to overcome the profile drag created by the wings as they are flapped. Since the speed and direction of the relative airflow alters along the length of a flapping wing, the calculation of profile power is very complicated. Detailed calculation on a strip analysis basis by Pennycuick (1968b) revealed that in the case of the pigeon (Columbia livia), the profile power was fairly constant between speeds of 3 and 18 metres per second. On the basis of this finding, Pennycuick (1975) concluded that profile power, since it was independent of speed, could for the sake of simplicity, be considered as a fixed multiple of the absolute minimum power (Pam). However, in accordance with the theory of Rayner (1979), Pennycuick (1968b) found that the profile power of the pigeon did increase with speed, although only at speeds above $18msec^{-1}$. Since the estimation of the factors which effect high speed flight performance is particularly important in this study it was decided not to employ the simplification presented in Pennycuick (1975) in order that the factors which determine the profile power, as originally calculated by Pennycuick (1968b), could be studied.

It is evident from the equations in the strip analysis presented by Pennycuick (1968b) that the profile power, when calculated in this way, depends heavily on the wingspan and the wing area. Pennycuick (1968a) in a study of the gliding flight of pigeons in a wind tunnel, found that as gliding speed increased, pigeons flexed their wings which resulted in lower wingspans. Since total drag, after subtraction of the estimated drag of the feet, was found to decrease with speed up to speeds of $18msec^{-1}$ and since induced drag (and hence induced power from equations (1) and (10)) was increased by this decrease in wingspan, Pennycuick concluded that reduction of wingspan must have resulted in a decrease in profile drag and hence profile power. In the strip analysis of the flapping flight of the pigeon, Pennycuick, (1968b), suggested that the increase in profile and hence total power required in flapping flight at speeds above $18msec^{-1}$ could be delayed by reduction of the wing area. Thus it would appear that a small wingspan and a small wing area are beneficial in reducing profile power, particularly at high speeds. This idea is supported by a study of the effect of wingspan on gliding performance by Tucker (1987). Tucker (1987) states that above a certain critical speed, wingspan and consequently wing area should decrease as speed increases in order to attain maximum performance levels.

Withers (1981) found by means of multiple regression that wing camber, which is the degree of arching of the wing, was the morphological parameter of the wing which best predicted the

coefficient of profile drag (CDpro). Wing camber was positively correlated with CDpro, r=0.71. This implies that the lower the wing camber ie the flatter the wing, the lower is the profile drag and hence the profile power required to overcome it. Withers (1981) also found that aspect ratio (Ar), the ratio of the wingspan (b) to the wing area (S) which is given by the equation

$$Ar = b^2/S \qquad (5.17)$$

was negatively correlated with CDpro (r=-0.54). This implies that the higher the aspect ratio the lower the profile drag and hence profile power.

Norberg (1986) states that in the case of bats, a long pointed wingtip reduces wing inertia and induced and profile powers while a short and broad wingtip enhances manoeuvrability.

d) Inertial power

Another component of power associated with flapping the wings is the power required to accelerate and decelerate the wings at the beginning and end of each stroke. For various reasons Pennycuick (1975) concluded that for the purposes of performance prediction, the inertial power need not be accounted for separately, provided that only medium and high air speeds are considered.

e) Basal metabolism

Pennycuick (1975) assumed that this component of power is equivalent to the standard metabolic rate of Lasiewski and Dawson (1967), and re-expressed their equation for non-passerines as

$$IIm = 3.79.M^{0.723}, \qquad (5.18)$$

where IIm is a power input ie rate of consumption of chemical energy, and M is the body mass in kilogrammes. Since the basal metabolism is assumed to be independent of speed, it can be added into the total power as a multiple of Pam. In order to do this, it must first of all be converted into an equivalent mechanical power (Pm) where

$$Pm = n.IIm, \tag{5.19}$$

where n is the mechanical efficiency of the muscles and supporting systems. Pm can now be expressed as a multiple of the absolute minimum power by the equation

$$Pm = X2.Pam, \tag{5.20}$$

where X2 is the metabolic power ratio. Combination of equations 5.18 and 5.19 yields the relationship

$$Pm = \alpha.n.M,^{\delta} \tag{5.21}$$

where α and δ are constants. Substitution for Pm from equation 5.21 and for Pam from equation 5.14 into equation 5.20 yields the relationship

$$X2 = \frac{6.03.\alpha.n.p^{1/2}.b^{3/2}.M^{(\delta-5/3)}}{k^{3/4}.g^{5/3}}, \tag{5.22}$$

where the values for α and δ for non-passerines are given in equation 5.18.

f) Ventilation and circulation power

From Tucker (1973) the mechanical power required for the heart to pump the blood is 5% of the total power required to fly, and the same is true for the power required to ventilate the lungs. Thus when all

the various power components outlined above have been summed, an additional 10% must be added to account for these requirements.

Bringing together the various components of the power required to fly which have been outlined above, an equation can be derived which gives the power required to fly horizontally (P) as a function of forward speed (V) as follows

$$P = 1.1\left(\frac{0.877k^{3/4}W^{3/2}A^{1/4}}{\rho^{1/2}\,Sd^{3/4}} \cdot X2 + \frac{kW^2}{2\rho SdV} + 1/2\rho AV^3 + Ppro\right). \quad (5.23)$$

When a plot of power required against forward speed is drawn for any real bird the result is a "U" shaped curve similar to but somewhat higher, due to the addition of the other power requirements outlined above, than that for the ideal bird which is presented in figure 2 of Pennycuick (1975).

Every species of bird has a given amount of power which its flight muscles can generate continuously (P_{ac}) and an absolute maximum amount of power which it can generate in short bursts (P_{max}). Both of these maximum power outputs can be represented by horizontal lines on the power versus speed curve at the appropriate level on the y-axis (Pennycuick 1968b figure 12). The points where these lines intercept the power curve define the maximum and minimum speeds at which the bird can fly either continuously or in short bursts. The power which is available either for climbing at a given speed or accelerating in horizontal flight from an instantaneous speed V, is equal to the difference between the maximum mechanical power output of the muscles (either continuously or in short bursts) and the power required for

flight at that speed.

A bird which is adapted for high speed flight and rapid acceleration, should be designed in such ways as to result in the intercept of the line of power available and the curve of power required being shifted to the right. This can be achieved by reducing the power required to fly at any speed, and hence the level of the power curve, particularly at high speeds.

2) Morphological features which influence the power required to fly

From the information given above the power required to fly could be reduced in the following ways:

a) Possession of a large wingspan and hence large disc area along with a low body mass resulting in a low disc loading (Q_d) given by the equation

$$Q_d = \frac{W}{Sd}. \qquad (5.24)$$

From equation 5.23 this results in lower induced and metabolic powers.

b) Possession of a small equivalent flat plate area (A). From equation 5.23 this would result in lower parasite and metabolic power.

c) Possession of high aspect ratio wings of short wingspan and small wing area with little camber and long pointed tips in order to reduce the profile power.

Clearly these different adaptations are not compatible with each other and may conflict with adaptations to increase power output which are outlined below.

An increased capacity for high speed flight and acceleration can also be achieved by increasing the power available, which would have the effect of raising the level of the power available lines in figure 12 of Pennycuick (1968b). In order to predict how power available could be increased it is necessary to understand the factors which influence power output.

3) Morphological features which influence the power output possible

In real life, a bird which is flying in still air must flap its wings in order to remain aloft. In general a bird flying horizontally at any particular speed can alter its wing beat frequency within certain limits which are defined by specific maximum and minimum values. Hill (1950) has suggested that the upper limit of the frequency of vibration of any limb is set by the strengths of the muscles and tendons that accelerate and decelerate the limb at either end of the stroke. In a series of geometrically similar animals, the way in which the maximum oscillation frequency varies with the linear dimensions (l) of the animal can be deduced as follows.

The stress which can be withstood by muscles and tendons is dependent on the substances of which they are made and can, therefore, be assumed to be constant among birds. The force exerted by a muscle will, therefore, be proportional to the cross-sectional area of its attachment, and hence to the square of its length. Therefore, the moment (J) that the muscle exerts about the centre of rotation of the proximal end of the limb varies with the length cubed

$$J \propto l^3. \qquad (5.25)$$

The limb's moment of inertia (I) about its proximal end is given by the equation

$$I = (m_1 r_1 + m_2 r_2 + \ldots m_n r_n), \qquad (5.26)$$

where m_n is the mass of the nth chordwise strip of the limb from the shoulder and r_n is the flapping radius of this strip. Thus

$$I \propto l^5, \qquad (5.27)$$

so that the angular acceleration (w) that the muscle can impart to the limb varies inversely with the length squared

$$w = \frac{J}{I} \propto \frac{l^3}{l^5} = l^{-2} \qquad (5.28)$$

If the wing is assumed to accelerate steadily through a fixed angle then the time (T) taken for each stroke is inversely proportional to the square root of the angular acceleration, and therefore varies directly with the length

$$T \propto w^{-1/2} \propto l \qquad (5.29)$$

The maximum wing beat frequency (f_{max}) is inversely proportional to T and therefore varies inversely with the length

$$f_{max} \propto 1/T \propto l^{-1} \qquad (5.30)$$

Thus for a given wing area, the longer the wing the lower is the maximum rate at which it can be flapped. Since power is the rate of doing work, the maximum wing beat rate which is sustainable is important in determining the maximum power output of the bird.

The model developed by Pennycuick (1975) to determine the way in which the minimum wing beat rate in horizontal flight scales with size

is as follows. The model comprises a bird, which is travelling forward at some speed V, on which (for calculation purposes) the following are assumed:

a) The wing is rectangular with semi-span 1/2b and chord length c.
b) The induced velocity (V_i) is small compared with the forward speed (V) and can be neglected when calculating the relative airspeed at a point on the wing.
c) The wings flap vertically up and down.

From this model (Pennycuick 1975 figure 11) it can be seen that the relative velocity denoted V_y at a chordwise strip, distant y from the shoulder joint, is the resultant of its horizontal velocity V due to the forward movement of the bird and the vertical velocity (w^2y^2) due to the downward flapping of the wing. Thus

$$V_y = (w^2y^2 + V^2)^{1/2}. \qquad (5.31)$$

Since the vertical velocity due to the downward motion of the wing is proportional to $(w^2y^2)^{1/2}$ it can be seen that when y is small (ie on the inner wing), so is the vertical velocity, such that the major component of the relative velocity of the inner wing is due to its horizontal velocity. Thus the inner wing functions in the same manner as when the bird is gliding (Figure 5.1). On the outer wing however (ie the manus), the value of y is large, hence the major component of the relative velocity is the vertical velocity due to the flapping of the wing (Figure 5.2). The angle between the aerodynamic reaction q on a wing strip and the resultant air velocity across it always exceeds a

right angle by an amount which depends on the ratio of the strip's profile drag to the lift developed by it (Figures 5.1 and 5.2). The result of this is that the more distal parts of the wing (ie the manus) make a greater contribution to the forward force than the more proximal parts.

In a real bird, the wings do not flap directly up and down but flap downwards and forwards on the downstroke and upwards and backwards on the upstroke. The flexibility of the carpometacarpal or wrist joints allows the wingtips to sweep through greater arcs in each wingbeat than if the wings were rigid as in the model above (see Pennycuick 1968b figure 2). However, this does not mean that the flapping velocities of the wingtips in a real bird are any higher than if the wings were rigid. Indeed, analysis of the data presented in McGahan (1973) indicates that the flapping velocities of the wingtips of the Andean condor (Vultur gryphus) are slower in reality than if the wings were rigid. However, if the wings of a real bird were rigid the wingtips would have very large angles of attack on the downstroke and would probably stall as a result. The flexibility of the wrist joints allow the manus of each wing to cant downwards and forwards during the downstroke, and hence to maintain lower angles of attack than if the wings were rigid. In conjunction with this, the forces which act on the manus of each wing cause the individual primary feathers to twist as the wings are flapped downwards. This also results in the outerwings being canted downwards and hence maintaining relatively low angles of attack. In flight, the angle of attack of the wing effects

the ratio of the lift and drag developed. In general, the best lift to drag ratio is achieved at low angles of attack (Kermode 1962). Thus the canting of the manus of each wing results in a relatively high lift to drag ratio, which in turn means that at any given speed, the net aerodynamic reaction on the outerwings is directed in a more forward direction in a real bird, than if the wings were rigid (Figs 5.2 and 5.3). Thus the forward force generated per wing beat can be increased by devoting a larger proportion of the wing area to the manus.

Because birds' wings are cambered, the air which flows over the wing has to travel further and hence faster than that which flows underneath in order to meet at the trailing edge. The result of this is that the air pressure above the wing is lower than that below, as explained by Bernoulli's principle (Shevell 1983). Thus the feathers on a bird's wing are subject to forces which tend to bend them upwards. It is reasonable to assume that the possession of stiff flight feathers which are more able to resist these forces will improve the efficiency with which the work done by the flight muscles is transferred via the wings to the air by reducing the energy lost in bending of the feathers. Thus stiffer flight feathers should increase the propulsive force generated by each wingbeat.

Power output is also affected by various properties of the flight muscles. Bock (1974) states that "the only case in which weight or mass of muscles can be used as an index of muscle function or

adaptation is the comparison in closely related species of homologous muscles that do not differ greatly in size or shape". He cites the study by Spring (1971) on common murres (Uria aalge) and thick-billed murres (Uria lomvia) as an example of such a case. Given that it is legitimate to use muscle mass as an index of power output, when comparing homologous muscles in closely related species, then the larger the flight muscles relative to body mass the greater is the relative power output. This idea is supported by the findings of Marden (1987). Marden (1987) found that animals which had a high proportion of their body mass as flight muscles were capable of lifting greater loads and taking off at steeper angles than animals with relatively smaller flight muscles.

In bird flight the pectoralis major muscles power the downstroke which is the propulsive phase of the wingbeat cycle and the pectoralis minor muscles power the upstroke which, at least at medium and high speeds is a passive recovery phase. Brown (1951), quoting Legal and Reichel (1880), states that the ratio between the weights of the pectoralis minor and major muscles was 3 to 1 and 4 to 1 in a partridge (Family Phasianidae) and pigeon (Family Columbidae) repectively, and 18 to 1 and 54 to 1 in a buzzard (Family Falconidae) and falcon (Family Falconidae) respectively. Brown (1951) concluded that the differences between these species were due to the fact that the partridge and the pigeon were strong fliers while the latter two species were habitual soarers which employed the elevator muscles very little. On the basis of these figures it would seem reasonable to

conclude that the lower is the ratio between the masses of these two muscles, the greater is the power of the flight of the bird. This does not necessarily mean that birds with relatively large pectoralis minor muscles can generate more thrust on the upstroke than birds with relatively smaller pectoralis minor muscles, since this capacity depends on the kinematics of the upstroke (Aldridge 1987). However, relatively large pectoralis minor muscles may allow the upstroke to be completed more rapidly and hence increase the frequency of the thrust generating downstrokes and hence the power output.

From the information given above a bird which is adapted for high speed flight and acceleration could increase the power available in the following ways:

a) Possession of relatively short wings of small area in order to reduce wing inertia and allow higher wing beat rates.

b) Possession of a larger proportion of the wing area as the manus in order to increase the forward force generated per wing beat.

c) Possession of stiffer flight feathers in order to increase the efficiency of the wings in propelling the bird.

d) Possession of large flight muscles relative to body mass.

e) Possession of large pectoralis minor muscles relative to the mass of the pectoralis major muscles.

4) Morphological features which influence manoeuvrability

Howland (1974) showed that the ability of a predator to catch its prey depended not only on the speed of which it was capable but also

on its manoeuvrability. As a measure of manoeuvrability Howland (1974) investigated the radius of turn which the predator could achieve, and found that the smallest turning radius of an animal could be found from the equation

$$r = k.M/A, \tag{5.32}$$

where r is the radius of turn, k is a constant, M is the mass of the animal and A is the area of the control surface used to cause the turn. In birds the area of the control surface is equivalent to the area of the wings. From this equation it is clear that the lower the ratio of mass to wing area, which is referred to as the wing loading, the smaller is the radius of turn possible. In an analysis of soaring performance in thermals, Pennycuick (1971) found that the radius of turn in a thermal is directly proportional to the wing loading and is given by the equation

$$r = \frac{W}{S} \cdot \frac{2}{pgC_l \sin\phi}, \tag{5.33}$$

where W is the weight, S is the planform area ie the area of the wings and the body in between, p is the air density, g is the force due to gravity, C_l is the lift coefficient and $\sin\phi$ is the angle of bank. It follows from this equation that at any given lift coefficient and angle of bank that the lower the wing loading (W/S) the tighter will be the turn possible.

As mentioned previously, Norberg (1986) stated that a short broad wingtip enhances manoeuvrability.

The manoeuvrability of a bird is enhanced by the speed of which it is capable and by the possession of powerful flight muscles which can act strongly and rapidly on the flying surfaces.

The tail of modern birds is used primarily to help to maintain lift at very low forward velocities in both gliding and flapping flight (Pennycuick 1975). However, in many species the tail is also used in fine control during flight by correcting small errors in pitch and yaw. Brown (1961) states that greater manoeuvrability can be associated with a tail which is both large and long, to increase the effective surface area, and which consists of stiff feathers that will be of benefit in the same manner as stiff remiges.

From this information it can be seen that a bird which requires to be agile could increase its manoeuvrability in the following ways:

a) Possession of a low wing loading to make tight turns possible.

b) Possession of a short broad wingtip.

c) Possession of large flight muscles relative to body weight.

d) Possession of a long tail of large area.

e) Possession of stiff tail feathers.

It is possible to make use of the information presented above to predict how skuas should differ from gulls if they are structurally adapted for more efficient kleptoparasitic flight. However, such predictions depend on the way in which it is assumed that kleptoparasitism is performed. This point is discussed in the following chapter.

Chapter 6

Morphological comparison of gulls and skuas.

Introduction

The morphological study which is described in this chapter was carried out to test the hypothesis that the morphology of skuas as "specialist" kleptoparasites differs from that of their closest relatives, the "opportunistically" kleptoparasitic gulls (although see Hoffman 1984), in ways which mean that skuas are better adapted for carrying out successful aerial kleptoparasitic attacks. Whether such differences reflect specialisations which evolved to enhance the kleptoparasitic success of skuas during an "asymmetric evolutionary arms race" (Dawkins and Krebs 1979, Furness 1987b) between skuas and their kleptoparasitic hosts, or merely represent morphological pre-adaptations which were a pre-requisite for the development of "specialised" kleptoparasitic feeding behaviour by skuas is discussed.

On the basis of the information given in the previous chapter various a priori predictions were made with regard to the morphological differences which should exist between skuas and gulls, as "specialist" and "opportunist" kleptoparasites respectively, if the hypothesis presented above is true. The suggestion of Brockman and Barnard (1979) that skuas and frigatebirds are morphologically adapted to feeding kleptoparasitically was made in reference to the use of high speed flapping chases which involve great feats of agility. Not all chases by skuas are of this type (see chapter 2), but

for the sake of simplicity, the predictions were made on the assumption that they are. The possibility that the morphology of skuas might deviate from these predictions because they use alternative methods of attack is discussed.

The three aspects of flight performance in which skuas were expected to be superior to gulls were the ability to fly fast, to accelerate to high speeds and to be more agile in the air. The three basic ways in which it was expected that skuas would achieve these ends were to reduce the power required to fly, particularly at high speeds, to increase the power available and to increase their manoeuvrability. Therefore, the morphological differences which should exist between gulls and skuas are as follows:

1) Skuas should have lower disc loadings than gulls of the same size. This would reduce the induced and metabolic power requirements (Eqn 5.23) and hence the total power required to fly, especially at low speeds. With a given maximum level of power available, this would result in more excess power for acceleration and allow a higher maximum flight speed.

2) Skuas should have lower wing loadings than gulls of the same size. This would allow them to make tighter turns (Eqns 5.32 and 5.33).

3) Skuas should have longer wings than gulls of the same size. This would result in lower disc loadings (Eqn 6.3) which would be of benefit as described in 1.

4) Skuas should have wings of larger area than gulls of the same size. This would result in lower wing loadings (Eqn 6.2) which would

be of benefit as described in 2.

5) Skuas should have shorter wings than gulls of the same size. This would result in a reduction of the profile power requirements and hence the total power required to fly, especially at high speeds. With a given maximum level of power available this would result in more excess power for acceleration and allow a higher maximum flight speed. In addition, relatively short wings would reduce the wing inertia (Eqns 5.25 - 5.27) and allow for a higher maximum wing-beat rate (Eqns 5.28 - 5.30). This would increase the maximum power output possible and, with a given level of power required, result in greater excess power available for acceleration and allow a higher maximum flight speed.

6) Skuas should have wings of smaller area than gulls of the same size for the same reasons as those listed immediately above.

7) Skuas should have higher aspect ratio wings than gulls. This would result in a reduction of the profile power requirements and hence the total power required to fly, especially at high speeds. With a given maximum level of power available this would result in more excess power for acceleration and allow a higher maximum flight speed.

8) Skuas should have less highly cambered wings than gulls for the same reasons as those given immediately above.

9) Skuas should have longer, more pointed wing tips than gulls for the same reasons as those given immediately above.

10) Skuas should have shorter, broader wing tips than gulls to enhance manoeuvrability.

11) Skuas should have more streamlined bodies than gulls of the same size. This would result in a reduction in parasite power requirements (Eqns 5.11 and 5.12) and hence the total power required to fly, especially at high speeds. With a given maximum level of power available this would result in more excess power for acceleration and allow a higher maximum flight speed.

12) Skuas should have a larger proportion of the wing area as the manus than gulls. This would increase the forward force generated per wing-beat.

13) Skuas should have larger flight muscles in relation to body mass than gulls. This would increase the maximum possible power output and, with a given level of power requirement, result in more excess power for acceleration and allow a higher maximum flight speed.

14) Skuas should have larger pectoralis minor muscles in relation to the size of the pectoralis major muscles than gulls. This feature is characteristic of powerful fliers and may allow for higher maximum wing-beat rates. This would increase the maximum possible power output and, with a given level of power requirement, result in more excess power for acceleration and allow a higher maximum flight speed.

15) Skuas should have longer and larger tails than gulls of the same size. This would enhance manoeuvrability.

16) Skuas should have stiffer retrices and remiges than gulls of the same size. This would increase the effectiveness of the wings in

propelling the bird and the efficiency of the tail in controlling aerial manoeuvres.

It is unfortunate that some of these predictions are contradictory, for the likelihood of observing morphological differences between skuas and gulls which could be explained as adaptations of skuas to enhance their flight performance is increased. However, this situation is unavoidable given the conflicting requirements of different aspects of flight performance and the difficulty in determining the relative importance of for example increased manoeuvrability and reduced profile power to the skuas. Nonetheless, the possibility that skuas do not differ significantly from gulls in either direction in these cases validates examination of these features.

Methods

1) Measurements of gross morphology

Morphological measurements were taken on a number of corpses which had been obtained from various sources. The corpses of the herring gulls (Larus argentatus), lesser black-backed gulls (Larus fuscus) and great black-backed gulls (Larus marinus) were obtained from licensed culls. The common gull (Larus canus) and the three Arctic skuas (Stercorarius parasiticus) were all found freshly dead from natural causes. Corpses of great skuas (Catharacta skua) were either obtained from licensed culls in Shetland or were found freshly dead from natural causes. All specimens were collected during the early part of

the breeding season, and only birds in normal body condition were used.

The morphological measurements which were taken on each specimen, when possible, were as follows:

a) Mass (m). Measured with a Pesola spring balance to the nearest 5g.

b) Wingspan (b). The distance between the two wingtips when the wings are spread to their absolute maximum extent.

c) Tail length. The distance from the base of the uropygial gland to the tip of the central tail feathers.

d) Outer-tail length. The distance from the point of insertion to the tip of the outermost tail feather.

e) Hand-wing length (l^{hw}). The length of the hand-wing (ie from the carpometacarpal joint to the wingtip).

f) Wing camber. Obtained by placing the specimen on its back and pinning out one wing in a spread position with an awl through the carpal joint. A small hook with thread attached was then looped round the leading edge of the wing and the distance to the trailing edge measured across both the upper and lower surfaces of the wing. This was done at two points on the wing (Fig 6.1). The wing camber along these two lines was determined by dividing length x by length y (Fig 6.2) while the wing camber of the whole wing was defined, in this study, as the mean of these two measurements.

g) Planform area (S). This is the projected area of both wings including the area of the body between the wings (Fig 6.3). This was measured by spreading one wing to its maximum extent over a sheet of

paper, such that the leading edge of the manus lay in a straight line with the leading edge of the inner wing, and tracing the outline. This outline was extended to the body midline by measuring a distance of 1/2 b from the wing tip (Fig 6.4). Total planform area was measured by cutting out and weighing the wing outline and converting paper weight into area by calculation based on the weight of a piece of paper measuring 100 square cm.

h) Percentage of wing area as the manus. This was defined as the area of the wing distal to a line joining the carpometacarpal joint and the boundary between the most distal secondary and the most proximal primary at the trailing edge of the wing (Fig 6.4). In this instance wing area does not include the area of the body between the wings.

i) Tail area. This is the projected area of the tail when spread to maximum extent such that the outer edges of the two outer tail feathers form a straight line perpendicular to the longitudinal axis of the body. This was measured by tracing and then weighing the outline of the spread tail and converting paper weight into tail area by comparison with a known standard.

j) Mass of flight muscles. The pectoralis major and pectoralis minor muscles were dissected from both sides of the body and weighed to the nearest 0.1g. From the masses of these muscles it was possible to calculate the mass of the pectoralis minor as a percentage of the mass of the pectoralis major, and the percentage of the total body mass as the main flight muscles.

k) Sternum length, keel depth, coracoid length, and sternum width. Measured with calipers according to the methods of Piersma et al. (1984), (Figs 6.5 and 6.6). Using these measurements, the standard muscle volume was determined from the equation

$$SMV = b\ (0.433c^2 + a.d). \qquad (6.1)$$

This equation, from Piersma et al. (1984), is derived from measurements on waders (Order Charadriiformes). As a second measure of flight muscle size the SMV value was expressed as a percentage of the average mass of the bird according to its sex and species. In this way any variation in muscle or body mass of individuals due to the presence or absence of fat and or protein reserves in each specimen was removed.

l) Humerus length. Measured with calipers or steel rule from the most proximal point of the head to the the most distal point of the ventral condyle.

m) Radius & Ulna length. Measured as above from the olecranon to the distal most point of the os carpi radiale.

n) Carpometacarpus and major digit. Measured as above from the most proximal point on the carpal trochlea to the tip of the major digit.

o) Carpometacarpus. Measured as above from the most proximal point on the carpal trochlea to the most distal point on the facet for the major digit.

p) Major digit. Measured as above from the most proximal point of the proximal phalange to the most distal point of the distal phalange.

All external measurements of length were measured to the nearest mm and all skeletal measurements were taken to the nearest 0.5 mm.

From the measurements described above the following morphological parameters were derived:

a) Wing loading (Q_S). Derived from the mass (m) and planform area (S) by the equation

$$Q_S = m.g/S, \tag{6.2}$$

where g is the acceleration due to gravity, 9.81 $msec^{-2}$.

b) Disc loading (Q_d). Derived from the mass (m) and the disc area (S_d) by the equation

$$Q_d = m.g/S_d, \tag{6.3}$$

where disc area (S_d) is derived from the wingspan (b) by the equation

$$Sd = \pi.b^2/4. \tag{6.4}$$

c) Linearized wing loading (LWL). Derived from the body mass (m) and the planform area (S) by the equation of Jaksic and Carothers (1985),

$$LWL = m^{1/3}.S^{-1/2}. \tag{6.5}$$

d) Hand-wing length index (HWLI). Derived from the hand-wing length (l^{hw}) and the wingspan (b) by the equation of Norberg (1986),

$$HWLI = 2.l^{hw}/b. \tag{6.6}$$

e) Aspect ratio (Ar). Derived from the wingspan (b) and the planform area (S) by the equation

$$Ar = b^2/S. \tag{6.7}$$

2) Statistical techniques

Analyses of the morphological data were carried out as follows. Bivariate regressions were calculated comparing body mass with each of the following variables; wingspan, central tail length, outer tail

length, tail area, planform area, wing loading, disc loading, humerus length, radius & ulna length, carpometacarpus & major digit length, carpometacarpus length, major digit length, linearised wing loading, hand-wing length index, wing camber, aspect ratio, the percentage of body mass as flight muscles, the mass of the pectoralis minor as a percentage of the mass of the pectoralis major, the standard muscle volume as a percentage of the body mass and the percentage of the wing area as the manus. For those variables which were expected to vary with body mass according to an allometric equation of the form

$$Y = B.X^k, \qquad (6.8)$$

ie the first twelve variables in the above list, common logarithms were used in the regressions against the common logarithm of mass. Those variables which were expressed as percentages and which were not expected to vary with body mass were tranformed by an arcsine transformation and regressed against body mass. The remaining variables ie. aspect ratio, wing camber, linearised wing loading and hand-wing length index were simply regressed against body mass.

Initially this was done for the complete sample of twenty eight gulls, which comprised thirteen herring gulls, ten lesser black-backed gulls, four great black-backed gulls and one common gull.

In order to test the validity of combining these four species of gull in one regression series, for subsequent comparison with skuas, it was decided to employ methods similar to those described in Hoffman (1984). For each variable which showed a significant correlation with

mass or logmass, for the sample of gulls, the correlation coefficient and least squares regression line were calculated for the sample of lesser black-backed gulls alone. To this sample each of the other three species of gull was added in succession and the new coefficient of determination (r^2) and the slope of the resultant regression (b) compared with those of the original regression. The rationale of this procedure, as explained by Hoffman (1984), is as follows.

When data are added that belong to the functional group defined by the original regression series, the statistics should respond in recognisably different ways than when data are added that do not belong to the functional group. If data are added that do belong, r (and hence r^2) should increase unless sample sizes are quite large. If a species is added that belongs to the functional group and that is outside the size range previously covered, r and r^2 will increase no matter how large the previous sample. As long as the species added belongs to the functional group, the slope b should not change significantly ie. the ninety-five percent confidence interval of the slope of the combined regression line should overlap with that of the original regression. On the other hand, if a species added to the regression series does not belong to the functional group (is differently proportioned), at least some of the regression slopes b should change significantly or the r^2 values should decrease, or both. Any change in r and r^2 between an original regression and the combined one can be attributed to the added data. Therefore, any decrease in r and r^2, however small, can be considered significant evidence that the

species added does not belong to the functional group, subject to two conditions. First, extremely small decreases in r^2 might result from rounding error in the calculations, and secondly, the sample from the added species must be assumed to be representative of the species.

The sensitvity of r^2 and b vary differently depending on the relative size of the species. If the added species is similar in size to the included species the slope is unlikely to change significantly but r^2 will decrease. If, however, the added species is markedly larger or smaller than those included in the regressions, r^2 will probably increase but the slope b should change.

When a test showed that a species deviated significantly from the functional group, the direction of the deviation was determined by substituting the mean body mass or the mean log body mass into the original regression equation and comparing the value predicted by that equation with the actual mean of the variable in question.

Having determined which species of gull to include in the gull regression for each variable, the samples of great skuas and Arctic skuas were added in turn to the sample of gulls and the resulting values for r^2 and the confidence intervals of the slopes of the regression lines compared with those of the original gull regression.

In the case of each of the variables which did not show a significant correlation with mass or log mass in the combined species gull sample, Kolmogorov-Smirnov one sample tests were carried out for each of the three larger species of gull in order to test for

deviations from normality. Where the assumption of normality was met Student's t-tests were carried out between each of the three larger species of gull and where no significant difference was observed between the species, the samples were combined. Kolmogorov-Smirnov one sample tests were then carried out on the multi-species gull sample and the sample of great skuas and the sample of Arctic skuas. Where the assumption of normality was met Student's t-tests were carried out for each variable between the multi-species gull sample and the sample of great skuas and then the sample of Arctic skuas.

Because great skuas covered only a small range of sizes which did not overlap with that of Arctic skuas, it was decided not to use the method of comparing single and combined species regressions to compare the morphology of these two species. Instead, variables which were expected to vary with either $mass^{1/3}$ or $mass^{2/3}$ were expressed as a proportion of these values and then transformed by an arcsine transformation. Arcsine transformations were also carried out on those other variables which were expressed as percentages. Kolmogorov-Smirnov one sample tests were carried out on each variable for both species and where the assumption of normality was met Student's t-tests were carried out to compare great skuas and Arctic skuas.

3) Measurements of feather flexural stiffness

The two outermost primaries (P9 and P10), the outermost tail feather (T6) and either the outermost secondary (S1) or the one proximal to it (S2), were removed from two herring gulls, two lesser black-backed

gulls, two great black-backed gulls, three great skuas, two Arctic skuas and one common gull.

The length of each feather was measured to the nearest 0.5mm and then the innermost vane was removed from the shaft. The shaft of each feather was then marked off at 5% intervals from the base to the tip and embedded to the 5% mark in a block of wood with araldite epoxy resin.

Bending tests were carried out by mounting the wooden blocks, in which the feathers were embedded, in a clamp stand. Deflections caused by suspending a given load from the shaft at every second mark along the length of the feather were measured, to the nearest 0.1mm, against a scale alongside the point of loading. Deflections were measured for two shaft orientations:

a) Shaft horizontal with ventral surface uppermost - to simulate the effect of higher air pressure below the feather.

b) Shaft horizontal along most of its length with leading lateral surface uppermost - to simulate the effect of oncoming air.

The weights which were used during the bending tests were selected in order that they would cause measurable deflections as close to the bases of the feathers as possible while being supportable by the feathers as close to their tips as possible. The weights which were selected were as follows:

a) 50g - primaries of great skuas, herring gulls, lesser black-backed gulls and great black-backed gulls.

b) 15g - primaries of Arctic skuas and common gull and secondaries and tail feathers of great skuas, herring gulls, lesser black-backed gulls and great black-backed gulls.

c) 5g - secondaries and tail feathers of Arctic skuas and common gull.

Since the deflection under a given load, measured at any fixed point along the length of a beam is dependent on the distance from the point of fixation, (Purslow and Vincent 1978), the deflection measured at, for example, a point half way along the length of a short beam will be less than that measured at the same point, relative to total length, of a longer but otherwise identical beam. The reason for this is that the point of loading will be further, in absolute terms, from the point of fixation in the longer beam. Thus it was necessary to convert the measured deflections into values standardised for the length of each feather. This was done by dividing an arbritary standard length by the actual length of each feather and multiplying the measured deflections by this conversion factor. In this way, deflections of the shorter feathers were scaled up and those of longer feathers were scaled down. The standard lengths which were selected to allow the conversion factors to be calculated were:

a) 30cm - primaries of all species studied.

b) 20cm - secondaries and tail feathers of great skuas, herring gulls, lesser black-backed gulls and great black-backed gulls.

c) 15cm - secondaries and tail feathers of Arctic skuas and common gull.

Since deflections under a given load increase distally along the shaft (Purslow and Vincent 1978), it was expected that any differences between species in the flexural stiffness of their feathers would be most pronounced at the tips of the feathers. Thus the comparisons between species were based on the deflections measured at the more distal points on the feather shafts rather than at the more proximal ones.

Results

1) Gross morphology

a) Comparison between gull species

Initially a series of least squares regressions was calculated for all variables for the whole sample of gulls (Table 6.1). Sixteen of the twenty variables showed a significant correlation with mass or logmass, including linearised wing loading, hand-wing length index, wing camber and the percentage of the total body mass as flight muscles, (none of which were expected to do so).

Of those sixteen variables, linearised wing loading, wing camber, the percentage of the total body mass as flight muscles and outer-tail length did not show a significant correlation with mass or logmass (as appropriate) when lesser black-backed gulls were considered alone (Table 6.2). Because the lesser black-backed gulls were all similar in size, the confidence intervals for the slopes of the regression lines were large.

On addition of the sample of great black-backed gulls to the lesser black-backed gulls, all the r^2 values increased (Table 6.3). This was

to be expected since these two species are markedly different in size. However, none of the slopes of the regression lines changed significantly. This seemed to indicate that lesser and great black-backed gulls were very similar in their morphology in spite of the large size difference. The only complication was in the percentage of the body mass as flight muscles. Although the confidence interval for the slope of the combined regression overlapped with that for the lesser black-backed gulls alone, the slope of the regression line changed from positive to negative on the addition of the great black-backed gulls. Thus it was decided to omit this variable from further analysis by the combined regression method.

When the single common gull was added to the regression series for lesser and great black-backed gulls, the r^2 values increased in all cases except that of wing camber (Table 6.4). Since the common gull was much smaller than either of the other two species of gull, it was expected that all values of r^2 would increase even if the common gull was slightly different in its morphology from the other two species. Thus it was decided to exclude the common gull from further analysis of wing camber by the combined regression method. In no case did the confidence interval of the slope of the combined regression differ significantly from that of the original regression. Again this implied close morphological similarity between the different species of gull.

Addition of the sample of herring gulls to the regression series for the other three species of gull produced surprising results (Table

6.5). In all cases the r^2 values decreased. This was clear evidence that herring gulls differ in their morphology from the other three species under consideration. The fact that none of the slopes of the regressions changed significantly was because herring gulls fall well within the size range covered by the other three species.

Substitution of the mean mass or mean logmass of the herring gulls into the original regression equations derived from the other three species revealed that all the wing elements and hence wingspan were shorter in the herring gulls than expected, and hence disc loading was higher. The mean planform area of the herring gulls was smaller than expected and hence wing loading and linearised wing loading were higher. The herring gulls had shorter hand-wing length indices ie less pointed wings, less cambered wings, and longer and larger tails than expected.

Having noted that there were differences between herring gulls and the other three species of gull, it was nonetheless decided to include herring gulls in the subsequent comparison between gulls and skuas. This decision was taken on the basis that, even with the herring gulls in the sample, the correlation coefficients were still very high in those variables which showed a significant correlation at all (Table 6.1).

Comparison between the three larger species of gull for the variables which showed no significant correlation with mass revealed no significant differences between the species apart from the relative size of the pectoralis minor muscles. It was found that the pectoralis

minor muscles were significantly smaller in relation to the mass of the pectoralis major muscles in the lesser black-backed gulls than in either of the other two species. The herring gulls and great black-backed gulls did not differ in this aspect of their morphology. Thus in the comparison of the relative size of the pectoralis minor muscles with skuas, lesser black-backed gulls were kept separate from the other two species of gull.

b) Comparison between great skuas and gulls

In fourteen of the fifteen variables considered, the addition of great skuas to the regression series for gulls, caused the value of r^2 to decrease and in seven cases, the slope of the regression line changed significantly (Table 6.6). It is obvious that great skuas and the gulls considered here differed significantly in their morphology. Substitution of the mean mass or mean logmass of the great skuas into the equations for the gull regressions yielded the following results. All of the wing elements and consequently the wingspan were shorter in great skuas than expected. Great skuas had shorter hand-wing length indices and shorter tails than expected. The tail area and planform area of great skuas were also smaller than expected while the wing, disc and linearised wing loadings and wing camber were all higher than predicted.

The results of the comparison between great skuas and gulls for those variables which did not show a significant correlation with mass for the combined species gull sample are presented in Table 6.7. The

aspect ratio and the proportion of the wing area as the manus were significantly lower in great skuas than in the gulls. The SMV as a percentage of body mass and the mass of the pectoralis minor as a percentage of the mass of the pectoralis major were significantly higher in great skuas than in the gulls. The percentage of the body mass as flight muscles was higher in great skuas than in the gulls, but not significantly so.

c) Comparison between Arctic skuas and gulls

Tables 6.8 and 6.9 contain the results of the comparison of Arctic skuas with gulls. Only in the case of the tail length, as measured from the uropygial gland to the tip of the central tail feathers, did the addition of Arctic skuas to the regression series for gulls cause the slope of the regression line to change significantly. This was obviously due to the greatly elongated central tail feathers of the Arctic skuas. Only in five of the other fourteen variables did the value of r^2 decrease on the inclusion of Arctic skuas. Substitution of the mean mass or mean logmass of the Arctic skuas into the original regression equations revealed that Arctic skuas had higher wing, disc and linearised wing loadings than predicted. However, Arctic skuas had shorter hand-wing length indices and less cambered wings than expected.

The mean aspect ratio of Arctic skuas was significantly higher than that of gulls as were the percentage of the body mass as flight muscles, the SMV as a percentage of the body mass and the mass of the pectoralis minor as a percentage of the mass of the pectoralis major

(in comparison with lesser black-backed gulls). The pectoralis minor muscles of the Arctic skuas were not significantly larger than those of the herring gulls and great black-backed gulls. The percentage of the wing area as the manus was significantly lower in the Arctic skuas than in the gulls.

d) Comparison of great skuas and Arctic skuas

Arctic skuas and great skuas differed significantly in thirteen of the twenty variables studied (Table 6.10). When standardised for body mass, the wing elements of Arctic skuas were significantly longer in all cases except the major digit. Consequently the standardised mean wingspan of Arctic skuas was significantly longer than that of the great skuas and the standardised disc loading significantly lower. The mean standardised planform area, wing loading and linearised wing loading were not significantly different. The mean hand-wing length index and mean standardised tail length, measured by either technique, were significantly longer in Arctic skuas than in great skuas, and the standardised tail area was significantly larger in Arctic skuas than great skuas. The mean aspect ratio of the Arctic skuas was significantly higher than that of the great skuas but the percentage of the wing area as the manus was not significantly different. Arctic skuas had significantly larger flight muscles than great skuas in relation to their mass since the percentage of the body mass as flight muscles and the SMV as a percentage of the body mass were significantly higher in Arctic skuas. The pectoralis minor muscles

were not significantly different in size between the two species.

2) Feather flexural stiffness

Although the sample sizes were small, it was felt that the very small intra-specific variation in the flexural stiffness of the feathers examined, obviated the need to sample any more birds. Indeed, the technique was so sensitive that the two primaries of one great skua and the outermost primary of one great black-backed gull which were markedly less stiff than the equivalent feathers of conspecifics which had been measured previously were, upon examination with a dissection microscope, found to have small splits in their shafts. The measurements of flexural stiffness of these feathers were discarded.

As can be seen from figures 6.7 to 6.22, the deflection curves for all the feathers of all species follow an exponential pattern. This reflects the increase in deflection under static load due to increasing distance along the shaft from the point of fixation and also the distally tapering design of the feather shafts. These results agree with those of Purslow and Vincent (1978).

The dorso-ventral and lateral flexural stiffness of the two outermost primaries, the outermost secondary and the outermost tail feather of both Arctic skuas exceeded that of the common gull, at least at the more distal points on the feather shafts, where any such differences were expected to be most noticeable, (Figs 6.7 to 6.14).

The dorso-ventral and lateral flexural stiffness of the outermost tail feathers increased sequentially from the lesser black-backed

gulls through the herring gulls and great black-backed gulls to the great skuas, (figures 6.19 and 6.20). This pattern was essentially repeated in the flexural stiffness of the two outermost primaries and the second outermost secondaries of these four species except that the primaries and secondaries of the great black-backed gulls were stiffer than those of the great skuas, (figures 6.15 to 6.18 and figures 6.21 and 6.22). In addition the dorso-ventral flexural stiffness of the secondaries of great skuas and herring gulls were almost identical, (figure 6.21).

Discussion

With their significantly higher disc loadings,relative to body mass, neither species of skua appears to be adapted to the reduction of induced power. However, since induced power is low at high speeds (Pennycuick 1975, Rayner 1979), this characteristic of skuas probably has little effect on their high speed flight performance relative to that of equivalently sized gulls.

Arctic skuas have a body morphology which is well adapted to the reduction of profile power in comparison with an equivalently sized gull. Their significantly shorter and broader wing tips are the only disadvantage in this respect. Thus the profile power required in flight by Arctic skuas is probably lower than that of equivalently sized gulls.

Great skuas were found to possess features which would reduce profile power (ie significantly shorter wings of smaller area), and

others which would increase profile power (ie significantly lower aspect ratio, higher wing camber and shorter and broader wing tips), and so probably require no less profile power to fly than gulls of equivalent size.

Since no measurements were made to calculate parasite power it is only possible to guess, on the basis of their general appearance, how the parasite power required by skuas differs from that required by equivalently sized gulls. In the field, Arctic skuas appear to be at least as streamlined, if not more so, than kittiwakes (Rissa tridactyla). Thus the parasite power of Arctic skuas is probably the same as , or possibly lower than that of gulls of the same size. Great skuas, on the other hand, are heavily built birds and appear no more streamlined in flight than gulls of comparable size. Thus the parasite power requirements of great skuas and gulls of the same size are probably similar.

Ignoring the fact that skuas have higher induced power requirements than gulls of the same size, on the grounds that induced power is unimportant at high speeds, it would appear that the power requirements at high speeds are lower in Arctic skuas than in gulls of the same size and similar in great skuas and equivalently sized gulls.

Purslow and Vincent (1978), predicted that since heavier birds need to generate greater forces to keep them airborne than lighter birds, the feathers of heavier birds should have greater resistance to bending. Therefore, any comparison between the flexural stiffness of

the feathers of different species must take into account differences in the weights of the species concerned. Since common gulls and Arctic skuas are almost exactly the same weight, allowing for the difference in the direction of sexual size dimorphism between the two species, Cramp and Simmons (1977), the differences in the flexural stiffness of their feathers cannot be explained by differences in the weight of the two species. Rather, the results indicate that Arctic skuas have relatively strong feathers for their size, in comparison with gulls.

If the relatively stiff flight feathers of Arctic skuas improve the efficiency of their wings in generating lift and thrust, then the Arctic skuas' significantly smaller proportion of the wing area as the manus, relative to that found in gulls, will be compensated. Therefore, given the significantly shorter and smaller wings, as indicated by the significantly higher disc and wing loadings, and larger flight muscles, the power output of Arctic skuas' should be higher than that of gulls of the same size.

In contrast to the comparison between the common gull and the Arctic skuas, the differences between the flexural stiffness under static load of the primaries and secondaries of the great skuas and the three large species of gull can be explained simply by differences in the weights of the species, with which the measured deflections show a completely inverse relationship. This finding agrees with the prediction of Purslow and Vincent (1978). The fact that the primaries and secondaries of the great skuas were stiffer than those of the

lesser black-backed gulls and herring gulls but less stiff than those of the great black-backed gulls, probably reflects the fact that great skuas are heavier than the former two species but lighter than the latter, Cramp and Simmons (1977). Thus there is no evidence that the flight feathers of great skuas are any stiffer than would be expected of a gull of exactly the same size. Therefore, contrary to expectations, the relatively small proportion of the wing area as the manus in great skuas would not seem to be compensated. Nonetheless, given the significantly shorter and smaller wings, larger flight muscles and larger pectoralis minor muscles it seems reasonable to conclude that great skuas are capable of greater power output than gulls of the same size.

It is, therefore, likely that the ability to fly fast and to accelerate to high flight speeds is greater in both species of skua than in gulls of the same size. This is likely to be true to a greater extent for Arctic skuas than for great skuas.

The relative aerobatic capabilities of skuas and gulls are difficult to assess quantitatively since most descriptions of features which are beneficial to agility are qualitative, for example Brown (1961) and Norberg (1986). In the one aspect of manoeuvrability which has been quantified (ie the minimum turning radius which a bird can achieve (Pennycuick 1971, Howland 1974)), both species of skua would seem to be less agile than gulls of the same size due to their higher wing loadings.

The fact that Arctic skuas and common gulls are the same weight and that great skuas are lighter than great black-backed gulls, implies that the relatively stiff tail feathers of Arctic skuas, in comparison with those of the common gull, and the relatively stiff tail feathers of great skuas, in comparison with those of the three large species of gull, including the great black-backed gulls, reflect a genuine difference between skuas and gulls, rather than any differences in size between the species.

If it is assumed that the relatively stiff tail feathers of skuas enhance the effectiveness of their tails in flight control, out of proportion to their physical size, then given the other features which skuas exhibit (ie their significantly shorter, broader wing tips and significantly larger flight muscles (particularly in the case of Arctic skuas)) it seems reasonable to conclude that certainly Arctic skuas and possibly great skuas are more agile than equivalently sized gulls.

Comparison of the morphology of Arctic skuas with that of great skuas showed that, with significantly longer and larger tails, lower disc loadings and significantly larger flight muscles relative to body mass, and significantly higher aspect ratios, Arctic skuas fit more closely the model of the "specialist" kleptoparasite suggested by the predictions listed in the introduction.

The overall picture which emerges is that Arctic skuas, with lower power requirements at high speeds, greater power available and greater agility than gulls of the same size, and great skuas, with similar

power requirements at high speeds, greater available power and possibly better manoeuvrability than gulls of the same size, are morphologically better adapted than similarly sized gulls, for high speed flight, acceleration and manoeuvrability. These findings support the hypothesis that the evolution of "specialised" kleptoparasitic behaviour either requires or has resulted in morphological adaptations which improve flight performance.

It is widely known that the flight capabilities of skuas and frigatebirds are well developed. Lofgren (unpbl) states that "no gulls can match similarly sized skuas in force, acceleration, flight speed and manoeuvrability" while Aymar (1936) states that "the skuas' flight, in its suggestion of reserve power, resembles that of an eagle rather than a gull". The flight capabilities of frigatebirds have been described as "outstanding" (Cramp and Simmons 1977).

The results of the morphological comparison between selected species of skua and gull would seem to support these statements, although on theoretical grounds the difference between the flight capabilities of skuas and gulls does not seem to be as great as was originally expected.

Even so, the fact that both the great and the Arctic skua differ significantly in various aspects of their morphology from gulls, poses the question, what is the reason for these differences? The fact that these differences mean that skuas are better adapted to the type of flight required for successful kleptoparasitism does not, however,

prove that these features evolved specifically for that purpose during an asymmetric evolutionary arms race between skuas and their hosts.

One of the major ecological differences between skuas and gulls is that skuas are highly migratory while most species of gull are not. Arctic skuas are trans-equatorial migrants which breed as far north as the Arctic tundra and winter around the coasts of South America, Southern Africa and Australia (Furness 1987a). Great skuas are extensive migrants when young and range as far afield as the northern coasts of South America and the coast of northwest Africa (Furness 1987a). Is it possible that the morphological differences between great and Arctic skuas and the species of gulls studied here reflect this important difference in their behaviour rather than differences in foraging behaviour? It is generally the case that migratory species have relatively longer wings than closely related non-migratory species (Hoffman 1984). This was found to be the case when the migratory lesser black-backed gull was compared with the closely related non-migratory (at least in Britain) herring gull (Fig 6.23). If the migratory habit of skuas has resulted in morphological differences from gulls then it would be expected that skuas would have relatively long wings in relation to body mass in comparison with a series of four species of gull, of which only one (the lesser black-backed gull) is highly migratory. The fact that both species of skua actually had shorter wingspans in relation to body mass than the series of gulls (although not significant in the case of the Arctic skua) would seem to refute the idea of the migratory habit of skuas

being the cause of the morphological differences from gulls. This idea is supported by the fact that both species of skua were found to differ from the sample of gull species in exactly the same manner in which the non-migratory herring gull was found to differ from the other three species of gull (ie higher wing loading and disc loading, shorter wingspan and smaller planform area).

Pennycuick (1987a) suggested that, at least in seabirds, migration is not an important factor in determining flight adaptations since migration simply requires the bird to forage in one direction instead of returning to its nest. Pennycuick (1987a) suggested that flight adaptations of seabirds are determined mainly by requirements of foraging and nest access. Since all species of skua and practically all species of gull nest in essentially the same sort of environment, from the point of view of nest access (ie on flat ground), any differences in the flight adaptations of skuas and gulls should reflect differences in their foraging requirements.

The relationship between foraging habits and flight adaptation in birds is poorly studied. Recent works on this subject are Spring (1971), Hoffman (1984) and Norberg (1986).

Spring (1971) found that thick-billed murres (Uria lomvia) had larger and longer wings in relation to their weight and relatively larger pectoral muscles than common murres (Uria aalge). On the basis of these findings, Spring (1971) concluded that thick-billed murres should be energetically more efficient if somewhat less manoeuvrable

fliers than common murres, and capable of generating greater propulsive force per wing beat. As regards the relative foraging capabilities of the two species, Spring (1971) concluded that the thick-billed murres' poorer agility would reduce their ability to catch mobile pelagic fish but that they would be more capable of maintaining a semi-stationary position by hovering which would allow them to hunt for low-mobility prey either within the water column or on the sea-bed. These conclusions agree with the findings of Swartz (1966) that fish were more common in the diet of common murres than in the diet of thick-billed murres which fed to a greater extent on benthic invertebrates. Nettleship and Birkhead (1985), in a review of the literature on murre feeding ecology, found this difference in diet between the two species of murre to be a consistent trend.

Hoffman (1984) found that within various sub-groups of the superfamily Laroidea there were good correlations between changes in feeding methods with size and the pattern of allometric scaling of wing-skeletal elements. Within a group of gulls of the genus Larus, and within the Family Stercorariidae, the larger species had proportionally shorter wings than the smaller species and were found to rely less on aerial foraging techniques than the smaller species. Within the Thalasseus terns, Sterna-sternula terns and a group of "hooded" gulls, larger species were found to have proportionally longer wings and to use the same feeding methods as the smaller species within each group.

Norberg (1986) found that birds and bats with similar ecological foraging modes showed strong convergence in wing shape. If the morphological evolution of "specialist" kleptoparasitic species was determined purely by the need to develop morphological features to enhance kleptoparasitic foraging performance it might, therefore, be expected that the effects of convergent evolution would be seen in distantly related "specialist" kleptoparasites. It is interesting, therefore, that the members of the two most commonly aerially kleptoparasitic families of bird, the frigatebirds and the skuas, are so markedly different in their morphology.

While both great and Arctic skuas have relatively short wings of small area with consequently high disc and wing loadings, frigatebirds have extremely long wings of large area in relation to their weight and consequently low disc and wing loadings. Frigatebirds also have much higher aspect ratios than skuas. Pennycuick (1983) gives a value of 12.8 for the aspect ratio of a magnificent frigatebird (Fregata magnificens). Even the tails of skuas and frigatebirds differ markedly, those of frigatebirds being extremely large, long and forked with elongated outer feathers while skuas' tails are small, particularly those of great skuas, with elongated central tail feathers.

It is difficult to reconcile these marked differences between skuas and frigatebirds with the idea that they have evolved under the same selection forces imposed by the requirements of successful kleptoparasitism. It seems more likely that these two families of

birds have evolved to completely different lifestyles yet still possess some essential features which give them great flight capabilities and hence the ability to be highly kleptoparasitic under particular conditions.

Of all the orders of birds, excluding those which contain the skuas (Order Charadriiformes) and the frigatebirds (Order Pelecaniformes), kleptoparasitism is most common in the Order Falconiformes (Brockman and Barnard 1979). The fact that the members of this Order (falcons, hawks, harriers and eagles (Family Falconidae)), which are all obviously morphologically adapted to and dependent on a predatory way of life, are frequently kleptoparasitic, indicates that the occurrence of this behaviour is not dependent on evolution for a kleptoparasitic way of life per se. Rather the occurrence of kleptoparasitism would seem to depend on both morphological adaptations, and a behavioural predisposition, to be predatory.

Pennycuick (1983) suggested that the wing shape of frigatebirds is the result of adaptations to soar in small thermals under trade wind cumulus clouds and to reduce the power required for flapping flight in order to minimise energy expenditure on occasions when thermals fail and flapping is essential. Because kleptoparasitism is such a conspicuous behaviour and often occurs close to land near the breeding colonies of the host species, the importance of this feeding technique to the kleptoparasite has often been exaggerated. Nelson (1976) states that, contrary to popular belief, frigatebirds feed mainly on flying-

fish and small squid for which they hunt by gliding and soaring above the sea and then catch either by pursuing over, or snatching from, the sea-surface while in flight. Since the ability to pursue and catch flying-fish requires high flight speed and great agility, and since many colonies of frigatebirds exist in areas where there are few potential victims to rob (Furness 1987a), it seems likely that the kleptoparasitic habit of frigatebirds is the result of morphologically and probably behaviourally pre-adapted species exploiting an alternative food source when it is possible and profitable to do so.

If this is the case for frigatebirds which are the archetypal "specialist" kleptoparasites, then the same is almost certainly true for skuas. Of all the species of skua, only the Arctic skua can be said to rely heavily on kleptoparasitism as a feeding technique. However, even Arctic skuas are not obligate kleptoparasites, for certain populations of this species breed well inland and are completely non-kleptoparasitic during the breeding season (Maher 1974). Maher (1974) showed that Arctic skuas which breed in Alaska feed mainly by predation of birds, particularly small passerines. Maher (1974) also showed that pomarine skuas (Stercorarius pomarinus) are obligate microtine rodent predators during the breeding season and that long-tailed skuas (Stercorarius longicaudus) are, by preference, also microtine rodent predators although capable of preying on passerine birds, juvenile shorebirds and insects. Furness (1987a) ranked the main feeding methods of each of the three species of the

Genus Catharacta. It appears that during the breeding season kleptoparasitism is an important feeding technique only to great skuas which breed in Iceland and the Faeroes.

Since skuas spend most of each year away from their breeding colonies, their biology outside the breeding season is probably important in terms of their overall ecology. Unfortunately the ecology of skuas during the non-breeding season is little known. However, the information which is available would seem to indicate that only in the case of the Arctic skua is kleptoparasitism the most important feeding strategy during the non-breeding season (Furness 1987a).

Given this information it seems unlikely that the morphological differences which were found between gulls and skuas are the result of adaptations which evolved specifically to enhance skuas' kleptoparasitic success rate during an asymmetrical evolutionary arms race with their hosts. This scenario would require that the skuas, having evolved from gulls to become "specialist" kleptoparasites with the concomitant morphological changes, have subsequently reverted to a much more "gull-like" feeding ecology of scavenging, predation and generally opportunistic habits to such an extent that only certain populations of one species of the whole skua family still depend heavily on the feeding technique for which they evolved in the first place, and then only during certain seasons of the year. This scenario is completely unsatisfactory from an evolutionary point of view.

Unlike gulls, all species of skua possess strongly hooked bill tips and a unique combination of webbed feet with strongly hooked claws on each toe. Hooked bills and claws are characteristic of predatory birds in which they are used for prey capture and dismemberment. Since the vast majority of kleptoparasitic interactions between skuas and their victims do not involve physical contact (see chapter 2) these features would seem to serve no useful purpose in terms of enhancing kleptoparasitic success. Thus the evolution of these characteristics by skuas is difficult to reconcile with the idea that the morphological differences between skuas and gulls are the result of evolutionary adaptations of skuas to a kleptoparasitic lifestyle.

However, even if the morphological differences between gulls and skuas cannot be ascribed purely to the evolution of morphological adaptations specifically for kleptoparasitism, it might be that this is the reason for interspecific morphological differences within the skua family.

The fact that Arctic skuas are more kleptoparasitic than great skuas and that they fit more closely the model of the kleptoparasite suggested by the predictions, might indicate differences in the degree of use of this feeding technique according to the degree of specialisation achieved. This would support the idea of morphological adaptations specifically for kleptoparasitism, at least within the skua family. However, several lines of evidence refute this idea.

Firstly, if this idea were correct, then it would be expected that the less well adapted species, which presumably use this feeding

technique less often than the better adapted species because they are less successful at it, would have a relatively low success rate when compared with the better adapted species under identical conditions. The results in chapter 2 show that this is clearly not the case since when chasing the same species at the same location, great skuas were almost invariably more successful than Arctic skuas in forcing their victims to release their fish.

Secondly the predictions which Arctic skuas were found to satisfy more than great skuas are based on the assumption that kleptoparasitic chases involve high-speed flight with vigorous flapping and rapid changes of direction. Such chases are typical of those performed by Arctic skuas (Taylor 1979, present study) but not of those performed by great skuas (Furness 1978a, present study). As mentioned in chapter 2, great skuas typically rely on gravity to gain speed, frequently do not flap their wings at all during chases and rarely make rapid turns while in pursuit of a victim.

Andersson and Norberg (1981) showed that in geometrically similar birds, the only aspect of flight performance, of importance in prey capture, which increased with predator mass was the terminal speed in a dive with either partly or completely folded wings. Since this is just the type of attack which great skuas typically employ (Furness 1978a, present study), it is interesting that great skuas are appproximately three times heavier than Arctic skuas, and therefore obviously better suited to this type of attack. Thus the difference in

morphology between great and Arctic skuas may reflect adaptations to different attack strategies rather than a lack of specialisation on the part of the less kleptoparasitic great skua.

Thirdly the difference in morphology between the two species of skua can be explained just as satisfactorily by differences in their feeding ecology without any reference to their kleptoparasitic tendencies. As mentioned previously, the main feeding technique of Arctic skuas, apart from kleptoparasitism, is predation of small, highly agile, passerine birds (Maher 1974). This feeding technique probably requires high speed flight and great agility. Great skuas in the northern hemisphere tend to prey on larger, less agile, seabirds such as auks (Family Alcidae) while the southern hemisphere members of the Genus Catharacta frequently prey on burrow-nesting petrels (Order Procellariiformes) at night on land, or on penguins (Order Sphenisciformes Family Spheniscidae) (see Furness 1987a for a review). Neither of these latter two feeding techniques require aerial pursuit and hence any need for speed or agility. Hence the fact that Arctic skuas seem to fit the model of a high speed, agile kleptoparasite better than great skuas may be the result of differences in their predatory habits rather than a lower degree of specialisation for kleptoparasitism on the part of the less highly kleptoparasitic great skua.

Thus even within the skua family, there would seem to be little evidence that morphological differences between species are the result of differing degrees of evolutionary adaptation specifically to

enhance kleptoparasitic success.

In conclusion, this morphological comparison between gulls and skuas has shown that both great skuas and Arctic skuas differ significantly from gulls in various aspects of their morphology. On theoretical grounds these differences should enhance the kleptoparasitic flight performance of skuas in relation to that of gulls of the same size. Hence, these findings support the hypothesis outlined in the introduction to this chapter.

However, there are several lines of evidence which refute the idea that these morphological differences between skuas and gulls, although beneficial to kleptoparasitic performance, are the direct result of an evolutionary "arms race" to enhance kleptoparasitic success as skuas evolved into "specialist" kleptoparasites. Rather the evolution of skuas from gulls can probably be better interpreted as the evolution of a family of birds with more predatory tendencies with the requisite evolution of superior flight capabilities. On the basis of this interpretation, the highly kleptoparasitic nature of skuas can be better explained as the result of behaviourally and morphologically pre-adapted species exploiting an alternative food source when it is possible and profitable to do so, as is the case in frigatebirds.

Chapter 7

Flight muscle histochemistry.

Introduction

The feathers and bones of a bird's wing are under the control of approximately fifty different muscles and muscle slips (George and Berger 1966). Of these, the pectoralis major and the pectoralis minor (supracoracoideus) muscles are the most important in depressing and elevating the humerus (and hence the whole wing) respectively.

It has long been known that different muscles have different contraction speeds. Pioneering studies on frog skeletal muscle (Sommerkamp 1928, Kruger 1929) revealed a correlation between fast and slow contracting components and a differentiation into histologically distinct fibre types.

George and Naik (1958) were the first to reveal a relationship between structure and function of avian muscle fibre types by histochemical demonstration of metabolic differences between the "red" and "white" fibres of the avian pectoralis muscle. "Red" fibres are adapted mainly for aerobic metabolism for rapid, fatigue resistant, continuous activity whereas "white" fibres are adapted mainly for anaerobic metabolism during short bursts of powerful activity (George and Berger 1966). Within the pectoralis muscles of birds, "white" fibres are typically found among birds, such as gamebirds (Order Galliformes) (Kiessling 1977), which employ bursts of very powerful rapid flight of short duration. Pigeons (Order Columbiformes) which

are also capable of rapid vertical take-offs (Pennycuick and Parker 1966), possess "white" fibres in their pectoralis major muscles (Talesara and Goldspink 1978). It has been shown that during periods of intense activity, it is these "white" fibres of the pectoralis major which are preferentially used (Parker and George 1973,1976).

Since kleptoparasitic chases are typically of short duration (see chapter 2) it could be imagined that, if skuas as "specialist" kleptoparasites are better adapted for executing short bursts of high speed chasing than gulls, "white" fibres should be present in skuas' but not gulls' pectoral muscles. This idea has been suggested previously by Pennycuick (1987a).

Recent studies (Reichman and Pette 1982, Green et al. 1984, Hintz et al. 1984, Pette 1985) have indicated that within both the classical "red" and "white" fibre types there is a wide range of enzyme activities such that many "white" fibres have higher aerobic oxidative potentials than many "red" fibres. Hintz et al.(1984) stated that, with a few exceptions, "all of the enzymes that we have examined and which are associated with either glycolytic or oxidative metabolism are present in different ATPase type II fibres" (ie fast "red" and "white" fibres) " in an unbroken continuum from high to low activity". They concluded that fast "white" glycolytic and fast "red" oxidative-glycolytic fibres are two extremes in a continuum.

Thus, even if the pectoral muscles of skuas do not contain classical "white" glycolytic fibres, it could be expected that the fibres which are present in their pectoral muscles should have a higher glycolytic

activity than those present in the pectoral muscles of gulls. Since "the level of glycolytic activity can be taken as an indication of the need to make fast and powerful contractions" (Rowlerson in prep.), a higher level of glycolytic activity in skuas' pectoral muscles would indicate a greater need to undertake such activity and presumably a greater degree of adaptation to doing so.

However, anaerobic metabolism is energetically less efficient than aerobic metabolism and results in the accumulation of an oxygen debt which must be "payed off" at some point in the future (Schmidt-Nielsen 1975). Davis and Guderley (1987) suggested that lactate accumulation as a result of anaerobic metabolism during dives would curtail puffins' (Fratercula arctica) and common murres' (Uria aalge) capacity for continued flight and feeding. Obviously it would be beneficial to skuas if they could carry out chases without having to resort to anaerobic metabolism. Therefore, adaptations to increase oxidative capacity may be more adaptive to skuas than an increased capacity for anaerobic metabolism. The pectoral muscles of hummingbirds have an extremely well developed oxidative capacity by virtue of the very large quantities of mitochondria and very high levels of oxidative enzymes present therein (Lasiewski et al. 1965, Grinyer and George 1969). Grinyer and George (1969) suggested that these features are adaptational for hovering flight and probably allow hummingbirds to hover continuously while using aerobic metabolism. Therefore, it was predicted that the fibres of the pectoral muscles of skuas should also

have a higher oxidative capacity than those of gulls. This would represent an adaptation, like that of hummingbirds, to allow high levels of activity to be carried out without necessarily incurring an oxygen debt.

This chapter details the histochemical examination and comparison of the fibres of the pectoralis major and pectoralis minor muscles of great skuas (Catharacta skua) and herring gulls (Larus argentatus). This is almost certainly the first description of the fibre composition of the flight muscles of great skuas, and possibly of any skua species.

Methods

1) Collection and preparation of muscle samples

All muscle samples were taken from adult birds which were culled under license, during the breeding season, for reasons of conservation or agricultural protection.

Within a few minutes of death, three small blocks of the pectoralis major muscle were removed. One of these (PMj1) was taken from the most superficial (ventral) surface of the muscle approximately mid-way along the length of the carina of the sternum and approximately mid-way along a hypothetical line, perpendicular to the long axis of the body, between the carina and the distal insertion of the muscle on the humerus. The two other blocks of muscle were removed from a more caudal and more medial position than PMj1. Block PMj2 was taken from a more dorsal (deeper) layer of the muscle than block PMj1, and block PMj3 from an even deeper layer, dorsal to block PMj2, but not

adjacent to the sternum itself. The pectoralis major muscle was then removed completely to reveal the pectoralis minor muscle. One superficial (ventral) block of muscle (PMn) was removed from the medial side of the central tendon of the pectoralis minor, approximately mid-way along its cranial-caudal length. The iliofibularis muscle was excised completely from the hind-limb and a block of this (Ilf) removed from the superficial surface of the "redder" part of the muscle.

These blocks of muscle were trimmed, sub-divided into smaller blocks and made into composite blocks of two muscle types. These composites were then mounted on pieces of cork sheet with OCT compound and rapidly frozen in isopentane cooled to circa -70°C in dry ice. These blocks were stored at -25°C until sectioned. Serial transverse sections were cut at 15 micrometre thickness in a cryostat maintained at circa -20°C and mounted on coverslips.

2) Histochemical procedures

a) Oxidative and glycolytic activity

Two of the most commonly-used metabolic markers for oxidative and glycolytic activity are nicotinamide adenine-dinucleotide tetrazolium reductase (NADH-TR) and alpha-glycerophosphate dehydrogenase (αGPDH) respectively. Serial sections of the muscle blocks were covered with one or two drops of the appropriate incubation medium (see for example Farber et al. 1956 for NADH-TR and Khan 1976 for αGPDH incubation solutions) at pH 7.5 and incubated in the dark at 37°C for 15-30

minutes for NADH-TR and for up to one hour for αGPDH. Sections were then rinsed in distilled H2O, dehydrated through a series of alcohols, washed three times in histosol and mounted on microscope slides with DPX mountant.

Since the studies of George and Naik (1958) new systems of fibre classification have been developed on the basis of variation in the intrinsic speed of shortening between different types of fibre. In studies of mammalian muscle it has been shown that the intrinsic speed of shortening of fibres is directly related to the activity level of myofibrillar adenosine triphosphatase (mATPase) ie the rate at which this enzyme liberates inorganic phosphorous from adenosine triphosphate (ATP) (Barany 1967, Barnard et al. 1971). A related property of this mATPase activity results in differences in its stability under acid and alkaline conditions. It is this factor that has allowed histochemical differentiation between fibre types on the basis of their speed of contraction. Generally, fibres which have slow rates of contraction stain less intensely than faster fibres once they have been exposed to alkaline conditions, while faster fibres stain less intensely than fibres with slower rates of contraction once they have been exposed to acidic conditions (Brooke and Kaiser 1969,1970, Guth and Samaha 1969,1970, Samaha et al. 1970). The systems of Guth and Samaha (1969,1970) and Brooke and Kaiser (1969,1970) were developed at the same time but used different terminologies, which recent studies (Green et al. 1982) have concluded are not entirely interchangeable since the correspondence between the two

classification schemes is not perfect. Depending on the types of fibres present in any given section, it is possible to classify these incorrectly when only acid or alkaline pre-treatment is carried out (Green et al. 1982). Thus it was decided to employ both of these histochemical techniques, in addition to the use of enzyme activity levels, to classify the fibre types present in the muscles of skuas and gulls.

b) mATPase activity

For the determination of the alkali pre-incubated mATPase activity the following procedures were employed: 1) Unfixed sections were pre-incubated at room temperature for 20 minutes in calcium / barbitone / acetate buffer adjusted to a pH of 10.5, 10.4 or 10.3 with acetic acid and/or sodium hydroxide solution; 2) washed once in distilled H2O; 3) washed once in calcium / barbitone / acetate buffer at pH 9.4; 4) incubated at 37°C for 30 minutes in calcium / barbitone/ acetate buffer containing ATP at pH 9.4; 5) washed once with calcium / barbitone / acetate buffer at pH 9.4; 6) washed three times with distilled H2O; 7) washed three times with 1%, 2% or 3% calcium chloride (CaCl2) solution; 8) washed twice with distilled H2O; 9) immersed for 3 minutes in 1% cobaltous chloride (CoCl2) solution; 10) washed four times in distilled H2O; 11) immersed in dilute ammonium sulphide solution; 12) washed three times in distilled H2O; 13) dehydrated through a series of alcohols with 2 minutes in each; 14) washed three times in histosol for 2 minutes each time; 15) mounted in

DPX mountant.

For the determination of acid pre-incubated mATPase activity the following procedures were employed: 1) Unfixed sections were pre-incubated for 5 minutes in 0.2M sodium acetate solution adjusted to a pH of 4.65, 4.55, 4.45 or 4.35 with acetic acid and/or sodium hydroxide solution; 2) washed twice in distilled H2O; 3) washed twice with calcium / barbitone / acetate buffer at pH 9.4; 4) incubated at 37°C for one hour in calcium / barbitone / acetate buffer containing ATP at pH 9.4; 5)-15) as above. Essentially these procedures were the same as those employed by Guth and Samaha (1969, 1970), Brooke and Kaiser (1969,1970) and Green et al. (1982).

3) Analysis of stained muscle sections

Stained sections were studied by light microscopy. As has been done in previous studies (Green et al. 1982), enzyme activities were judged on a subjective basis by eye. Fibre types were classified into several categories (see Table 7.1) according to staining intensities. The proportions of different fibre types present in each type of muscle were determined by sampling at least 400 fibres per muscle block. Mean fibre diameters were derived from samples of at least 100 fibre diameters which were measured with a calibrated ocular scale.

Results

The results presented in Table 7.1 are derived from one herring gull and one great skua. Unfortunately muscle block PMj2 of the great skua was not sufficiently well preserved to allow detailed analysis of the

proportions and sizes of different fibre types present at this site.

The use of samples of one is common practice in histochemical studies (see Rosser and George 1986) in which analyses are essentially qualitative. Due to the qualitative nature of the technique utilised to classify fibre types it was felt that the use of statistical analyses was not merited and hence that a sample of one member of each species was sufficient for the purposes of the present study.

Within all the different muscle blocks, with the exception of block PMj3 of the great skua, either two or three different fibre types could be distinguished (Table 7.1). The differentiation between different fibre types was most apparent in those sections which had been stained for mATPase activity following pre-incubation at pH 10.5 for the herring gull (Table 7.1, Figs 7.1 and 7.2) and at pH 10.3 for the great skua (Table 7.1). This difference between the two species reflects the different profile of pH sensitivity which the muscles of the two species exhibited (Table 7.1). This point is of no consequence as far as the relative metabolic capacities of the muscles of the two species are concerned and is merely a point which must be borne in mind when selecting the pH of pre-incubation solutions to be used during interspecific comparisons (Rowlerson in prep.).

Slow fibres, which stained poorly after alkaline pre-incubation and stained intensely after acidic pre-incubation, were found only in the iliofibularis muscles of the two species (Table 7.1). All other fibres stained poorly after acidic pre-incubation and showed complete

inhibition of mATPase activity at pH 4.45 - 4.35 (Table 7.1). Clearly these fibres were all of the fast contracting type (Brooke and Kaiser 1969, 1970, Talesara and Goldspink 1978, Green et al. 1982).

Fast twitch glycolytic (FG or "white") fibres exhibit a decrease in staining intensity between pre-incubation pHs of 4.6 and 4.3 and do not exhibit complete inhibition of mATPase activity until pre-incubated at pH 4.3 (Brooke and Kaiser 1970, Dubowitz 1974, Rowlerson in prep.). Since there were no changes in the intensity with which the fibres of the herring gull pectoral muscles stained over the range of pre-incubation pHs 4.65-4.45 and since the mATPase activity of all the fibres of the pectoral muscles of both species was completely inhibited at pH 4.45-4.35, it is felt that "white" fast twitch glycolytic fibres were not present in the pectoral muscles of either species (Table 7.1). It is concluded that, with the exception of the slow fibres present in the iliofibularis muscles of both species, all the fibres studied were of the fast twitch oxidative-glycolytic (FOG or "intermediate or red") type. This conclusion is supported by the measured fibre diameters (Table 7.1). George and Berger (1966) stated that in the same species, where two fibre types are present in the pectoral muscles, the diameter of the "red" fibres is always less than that of the other types ("intermediate" or "white"). All of the fibre types present in the pectoralis major muscles of both species had mean fibre diameters of 38 micrometres or less. Fast twitch glycolytic ("white") fibres of the pectoralis major usually have diameters in excess of 50 micrometres (George and Berger 1966, Talesara and

Goldspink 1978). All of the fibre types present in the pectoralis minor muscles of both species had mean diameters of 51 micrometres or less (Table 7.1). Fast twitch glycolytic ("white") fibres of the pectoralis minor muscle typically have diameters in excess of 60 micrometres and usually in the range of 70-95 micrometres (George and Berger 1966). Clearly the fibres of the flight muscles of the herring gull and the great skua were too small to be "white" fast twitch glycolytic fibres. Where two types of fibre were present in a block of the pectoralis major muscle, the mean fibre diameters of the two types were very similar (Table 7.1) and those with the lower oxidative capacity, which is characteristic of "intermediate" fibres (George and Berger 1966, Rosser and George 1986), were not always the larger of the two (Table 7.1). Therefore, it is felt that in both species, the areas of the pectoralis major muscles which were studied consisted entirely of "red" fast twitch oxidative-glycolytic fibres. In the pectoralis minor muscles of both species, the fibres which had the lowest oxidative capacity (as measured by staining intensity with NADH-TR) had the highest mean diameter of the types present (Table 7.1). Therefore, the pectoralis minor muscles of both herring gulls and great skuas may consist of approximately 70% "red" fast twitch oxidative-glycolytic fibres and approximately 30% "intermediate" fast twitch oxidative-glycolytic fibres.

In terms of the overall level of staining intensity and the proportion of fibres which stained most intensely, the levels of

oxidative and glycolytic activity were generally higher in the pectoralis major muscles than in the pectoralis minor muscles and higher in both of these muscles than in the iliofibularis muscles. Although this was true for both species (Table 7.1), the increased level of enzymatic activity in the pectoral muscles in comparison with the iliofibularis muscle was more marked in the great skua than in the herring gull (Table 7.1). Whereas the iliofibularis muscles of the two species showed the same range of staining intensities and approximately the same proportion of fibres with the lowest levels of enzyme activity (ie 24% for the herring gull and 17% for the great skua), the pectoral muscles of the great skua exhibited higher levels of oxidative and glycolytic enzyme activity than the equivalent muscles of the herring gull (Table 7.1). This conclusion is based on the generally higher staining intensities (under the metabolic markers NADH-TR and αGPDH) of the fibres in the pectoral muscles of the great skua compared with those of the herring gull (Table 7.1, Figs 7.3 and 7.4) and the trend for the proportion of fibres with the higher staining intensity in any given block of the pectoral muscles to be higher in the great skua than in the herring gull (Table 7.1).

Discussion

The finding that the pectoralis major muscles of the herring gull appear to consist solely of "red" fast twitch oxidative-glycolytic fibres is in accord with the results of Rosser and George (1986) who

also found the same to be true of the ring-billed gull (Larus delawarensis). If the small blocks of the pectoral muscles which were examined were representative of the whole muscle, then herring gulls and great skuas have the same distribution of fibre types in their pectoral muscles as does the house sparrow (Passer domesticus) ie 100% "red" fibres in the pectoralis major and approximately 70% "red" and 30% "intermediate" fibres in the pectoralis minor (George and Berger 1966).

The major finding of the present study is that, contrary to expectations, no "white" fast twitch glycolytic fibres were found in the pectoral muscles of the great skua. It appears that in this respect skuas are no better adapted than gulls for carrying out short bursts of high speed chasing using anaerobic metabolism.

Talesara and Goldspink (1978) and Rosser and George (1986) both suggested that slow fibres in the pectoralis major muscles of birds may be active primarily during gliding flight. Rosser and George (1986) also suggested that birds which indulge primarily in powered flight cannot "afford the luxury" of populations of slow fibres in the pectoralis muscles since the power requirements of flight are high and the pectoralis major muscles comprise a large proportion of the total body weight in any case. George and Berger (1966) stated that in the pigeon, it is likely that during continuous flight the "white" fibres remain passive. Hence, it seems reasonable to argue that skuas which undertake lengthy annual migrations, spend a great deal of their life in flight and rely primarily on flapping flight, cannot "afford

the luxury" of a population of "white" muscle fibres which would be inactive for the vast majority of the time. Those birds in which "white" fast twitch glycolytic fibres are numerous in the pectoral muscles, for example the domestic fowl (Gallus gallus) (George and Berger 1966, Kiessling 1977), the ring-necked pheasant (Phasianus colchicus) (Kiessling 1977) and the ruffed grouse (Bonasa umbellus) (Rosser and George 1986) spend the vast majority of their lives on the ground. Given that walking is less energetically expensive than flying (see chapter 3) it is likely that these types of bird are not under the same degree of selection pressure to minimise weight as are birds which fly a great deal, and hence can "afford" to have populations of "white" fast twitch glycolytic fibres in their pectoral muscles.

Perhaps the prediction that the pectoral muscles of skuas should contain "white" fibres was, so to speak, searching for an "idealised kleptoparasite" without taking into consideration all the other factors which play a role in compromising the morphology of all but the most highly specialised of birds. However, since both of the pectoral muscles of the great skua had higher levels of oxidative and glycolytic enzyme activity than the equivalent muscles of the herring gull, it appears that great skuas are metabolically better adapted than herring gulls to engaging in periods of intense activity such as occur during kleptoparasitic chases. Perhaps these features represent the most adaptive solution for skuas given that the possession of "white" fibres could be considered as an over-specialisation for

species which spend the vast majority of their lives engaged in activities other than kleptoparasitism.

It remains to study the fibre composition of the pectoral muscles of Arctic skuas (Stercorarius parasiticus). Since Arctic skuas rely on kleptoparasitism and the use of high speed flapping pursuits to a greater extent than great skuas (see chapter 2), the former might be more likely to have "white" fast twitch glycolytic fibres in their pectoral muscles than the latter. However, for the same reasons as have been given above this would probably be an overspecialisation for Arctic skuas as well.

The results of this histochemical study which have indicated that the flight muscles of great skuas are better adapted for high activity than those of herring gulls, bear out the anecdotal account of Aymar (1936) who stated that " the skuas' flight, in its suggestion of reserve power, resembles that of an eagle rather than that of a gull". This greater capacity for anaerobic and aerobic metabolism almost certainly enhances the ability of great skuas to carry out high speed kleptoparasitic chases, in comparison with herring gulls' ability to do so. Thus it could be argued that this difference in the level of enzyme activities between the two species has arisen because skuas have evolved adaptations specifically to enhance their kleptoparasitic flight performance. However, as discussed in the previous chapter, this difference between gulls and skuas could just as easily be a consequence of adaptations of the latter to a more predatory lifestyle than the former.

Chapter 8

Discussion.

There is no doubt that skuas and gulls are very closely related to one another. Skuas and gulls are more similar to each another in terms of overall size and shape than either are to any of the other members of the order Charadriiformes to which they belong.

Unquestionably, however, there are profound morphological differences between the two families. The morphology of skuas and gulls has been widely studied, but most comparative studies have been concerned with the taxonomic relationship between them (Hudson et al. 1969, Schnell 1970a,b, Hoffman 1984). In spite of the existence of numerous references to the outstanding flight performance of skuas (Aymar 1936, Berry and Johnston 1980, Cramp and Simmons 1983) when chasing other birds, only a very few studies have examined the morphology of skuas in relation to their flight capabilities (Hoffman 1984, Pennycuick 1987b).

The present study has indicated that in many aspects of their morphology skuas differ significantly from equivalently sized gulls in ways which, on the basis of the theory of flight, appear to benefit skuas', particularly Arctic skuas' (Stercorarius parasiticus), high speed flight performance. These results are consistent with the idea that skuas possess morphological adaptations to enhance their kleptoparasitic success.

Including the present study, three direct comparisons between the success rates of skuas and gulls chasing the same species at the same location have now been carried out; in all cases skuas were found to be more successful than gulls (Arnason and Grant 1978, Forssgren 1981, present study). Even although the majority of skua species are not highly kleptoparasitic, the possession of morphological features which enhance success rates is likely to confer advantages on them in certain situations. It is felt that these advantages are at least threefold.

The first potential advantage may benefit skuas, such as great skuas (Catharacta skua) in Shetland, which obtain the majority of their food by means other than kleptoparasitism. Interspecific and probably also intraspecific competition among great skuas has always been intense over surface shoals of sandeels (Ammodytes marinus) which even in the mid-1970s were unpredictable in their temporal availability and spatial distribution (Furness 1987a). Furness (1987a) suggested that non-breeding great skuas fed on whitefish discarded from trawlers to a greater extent than breeding birds because of intense competition which forced the non-breeders to make use of discards as a more easily obtainable but less profitable food source. However, interspecific and intraspecific competition between seabirds is also extremely intense behind whitefish trawlers (Hudson and Furness 1988). In this situation, great skuas are generally at a competitive disadvantage to gannets (Sula bassana) and great black-backed gulls (Larus marinus) (Hudson and Furness 1988).

With the current reduction in the availability of sandeels around Shetland and the use of nets with larger mesh size leading to a reduction in the quantity but an increase in the mean length of fish discarded by commercial fishing vessels, competition between great skuas and other species, and among great skuas, at sandeel shoals and behind fishing boats has probably increased. This may have reduced the profitability of these feeding techniques to all individuals or at least to those individuals which were at a competitive disadvantage in any case. Furness (1977) concluded that in the mid-1970s, scavenging, predation and piracy were time consuming and relatively unprofitable in comparison to the great skuas' main feeding techniques. However, with the probable reduction in the profitability of the latter it is likely that great skuas may turn increasingly to alternative feeding techniques (Hudson and Furness 1988) such as kleptoparasitism which may be relatively more profitable now than in the past. The present study has indicated that with their present kleptoparasitic success rate, great skuas could in theory collect food at a sufficiently high rate to allow successful reproduction. Thus when other food sources fail, the ability to be successful kleptoparasites, as a consequence of the possession of the appropriate morphological features, may allow skuas to continue to breed under conditions which would otherwise preclude successful breeding.

The second potential advantage of increased success rates, conferred by appropriate morphological adaptations, concerns species which feed

entirely by kleptoparasitism and have no alternative to feeding in this way, for example Arctic skuas in Shetland. O'Donald (1983) argued that because Arctic skuas spend very little time foraging per day, obtaining food was not a factor which limited Arctic skua breeding numbers in Shetland. For the same reason, O'Donald (1983) argued that differential success rates of light and melanic Arctic skuas could not explain the plumage polymorphism of Arctic skuas since individuals of the phenotype with the lower success rate could, with so much "spare time" available, increase their foraging effort to compensate if so required. However, birds may have to spend considerable periods of time resting each day, depending on the cost of their locomotion (Norberg 1977), in order to keep energy expenditure below a critical maximum sustainable level which Drent and Daan (1980) suggested was approximately four times BMR. Therefore, apparent idleness may not be so. Clearly any slight increase in success rate, conferred by morphological adaptations, which reduces the time required to collect a given amount of food, will reduce parental energy expenditure. Under conditions of food shortage, only birds with high success rates may be able to collect food in a short enough time to keep energy expenditure below the critical level and birds with poorer success rates may be unable to meet their chicks' food demands without risking reductions in parental survival due to excessive energy expenditure. Another benefit of reducing the time required to collect food through higher success rates is that under conditions of food stress, when adults are likely to need to leave their chicks unguarded

(Furness 1977, Barrett and Runde 1980, Galbraith 1983, Reid 1987, Pietz 1987, present study), the likelihood of them doing so is reduced.

In 1987 Arctic skuas on Foula never left their chicks unguarded during the pre-fledging period and appeared to be expending energy at rates just under four times BMR when rearing chicks. It is likely that if Arctic skuas on Foula had only been as successful as gulls were found to be, they would have had to; spend considerably more time foraging than they did, expend energy at a higher rate, leave their chicks unguarded and would probably have had even poorer rates of chick-growth and survival than they did.

In both of these situations discussed above the advantage to skuas of increased kleptoparasitic success rates due to possession of the appropriate morphological adaptations, will only be of apparent benefit under conditions of food shortage. This was one of the ecological conditions which Brockman and Barnard (1979) originally suggested would facilitate the evolution of kleptoparasitic behaviour.

It is apparent that in 1986 and 1987 skuas in Shetland were suffering from a shortage of food as evinced by their increased foraging effort, high rates of energy expenditure, tendency to leave chicks unattended, poor chick-growth and poor breeding success. Perhaps only in recent years have the advantages of increased kleptoparasitic success become effective in maintaining previously high breeding success, or merely slowing down what would otherwise

have been more dramatic declines in skua fortunes.

The three species of skua which belong to the genus Stercorarius are circumpolar in their breeding distribution (Furness 1987a). Of the three species, the most highly kleptoparasitic, ie the Arctic skua, has the widest breeding distribution and occurs as a breeding species on many of the islands throughout the Arctic and sub-Arctic regions where the other two small species of skua do not. Arctic skuas in Scotland are at the southernmost limit of their breeding range. At this latitude populations of small rodents are too low to support large colonies of skuas. Furness (1987a) suggested that the dependence of pomarine skuas (Stercorarius pomarinus) on small rodents, particularly lemmings, as a food source during the breeding season explains their absence as a breeding species from the whole of Europe. Furness (1980) suggested that Foula holds one of the largest breeding colonies of Arctic skuas in Shetland because of the large number of seabirds available to chase. Certainly the highest densities of Arctic skuas occur in Britain and the Faeroes where they feed largely by kleptoparasitism (Furness 1987a). Thus where Arctic skuas breed in the absence of the other two small species of skua, they tend to feed kleptoparasitically. Skuas may not be as successful as gulls in terms of worldwide breeding distribution or populations, but it seems possible that the possession of morphological features which enhance their ability to feed successfully by kleptoparasitism may allow skuas to breed in locations where there is no alternative to feeding in this way and hence to increase their breeding ranges beyond what would

otherwise be possible.

Although it has been suggested that the morphology and plumage of skuas have evolved to enhance their success as kleptoparasites (as a result of an "asymmetric evolutionary arms race" with their hosts), the data presented in this thesis give rather little support to this idea. The greater tendency of skuas to behave kleptoparasitically and their greater ability to feed successfully in this way seem largely due to pre-adaptations of the Family Stercorariidae which have arisen during the course of the evolution of skuas to a more predatory way of life than gulls.

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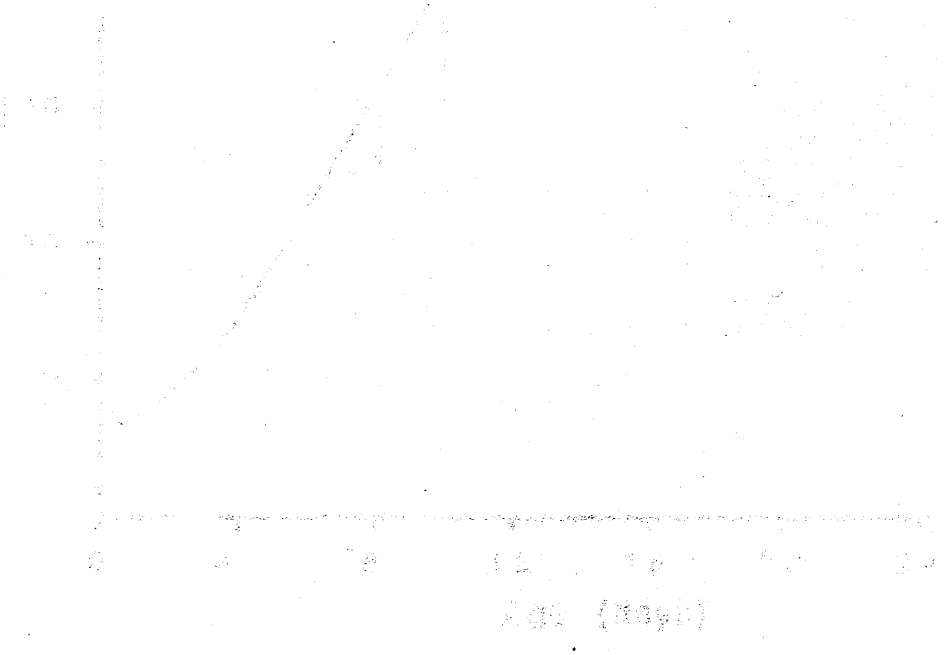


Fig. 4.1 Logistic growth curve of Arctic skua chicks of known hatching date (from Furness 1980) superimposed on plot of Arctic skua chick weight against age (1987 data).

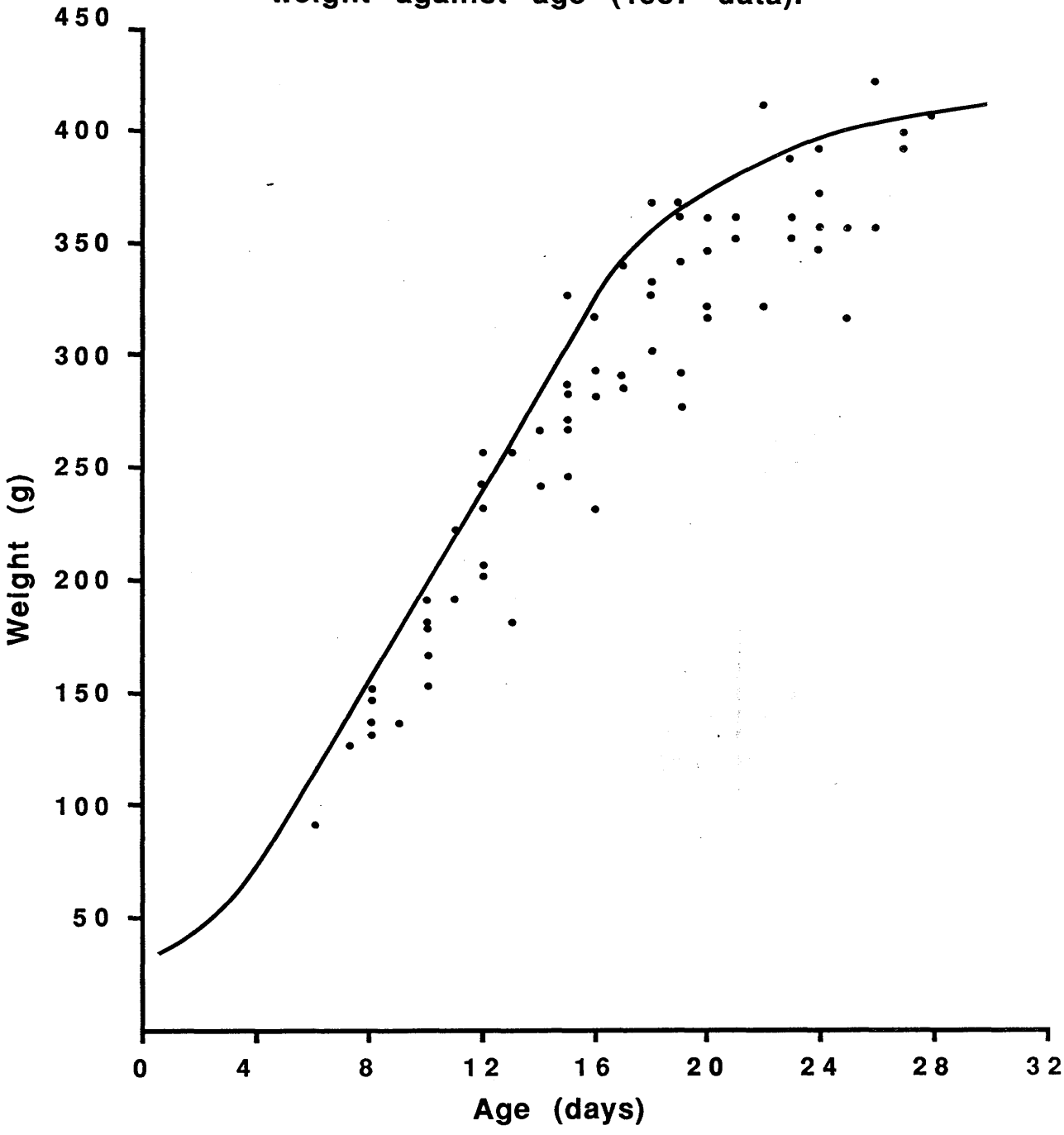
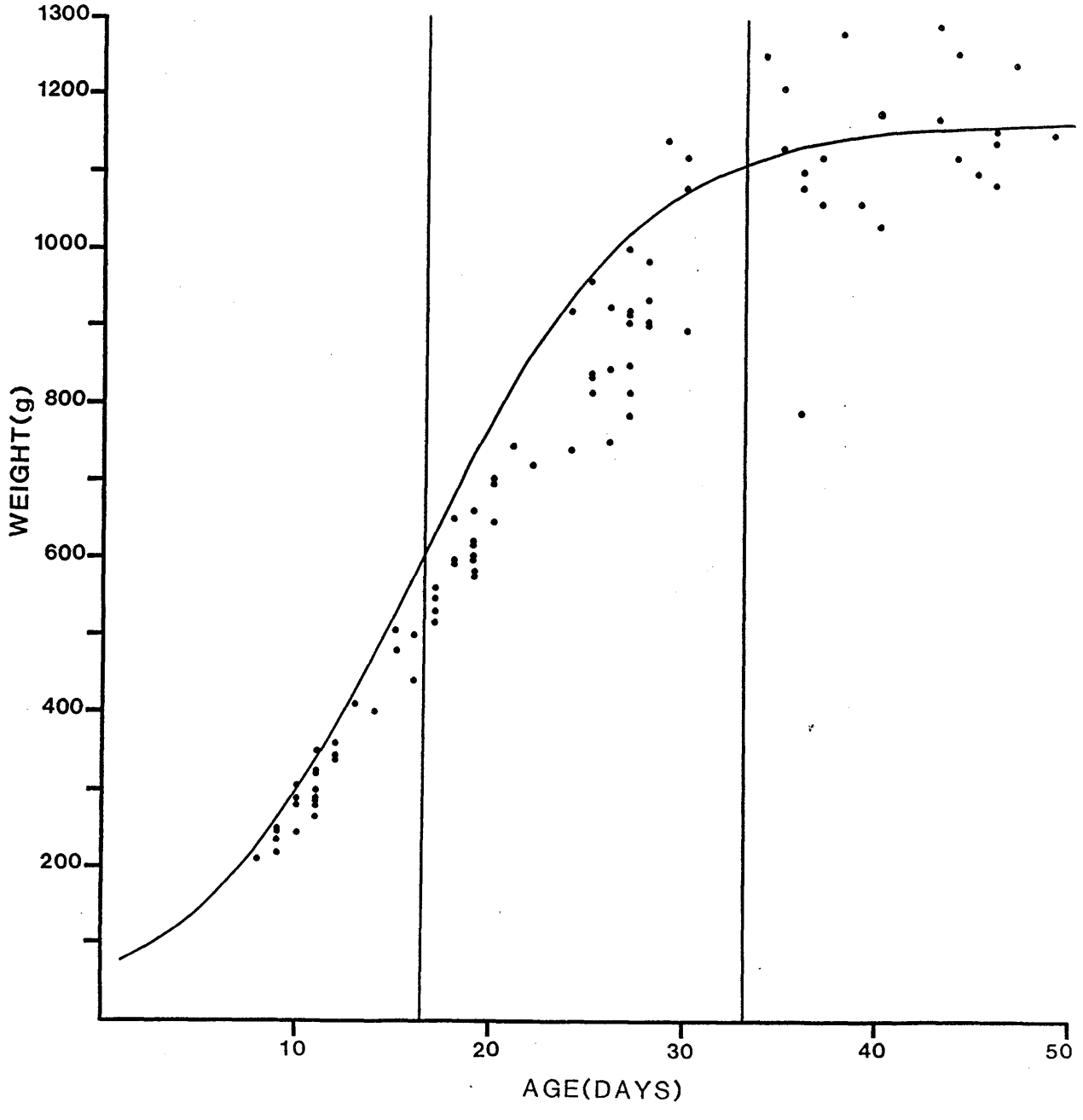


Fig. 4.2 Logistic growth curve of great skua chicks growing "typically" (from Furness 1977) superimposed on plot of great skua chick weight against age (1987 data).



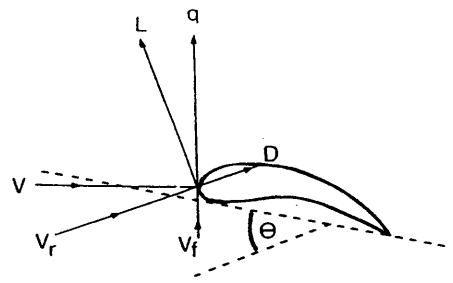


Fig 5.1. Local velocities and forces on the innerwing during flapping flight. Vr is the resultant of forward velocity V and flapping velocity Vf. Θ is the angle of attack (between the wing and the relative air flow). L and D are the lift and drag respectively and q is their resultant.

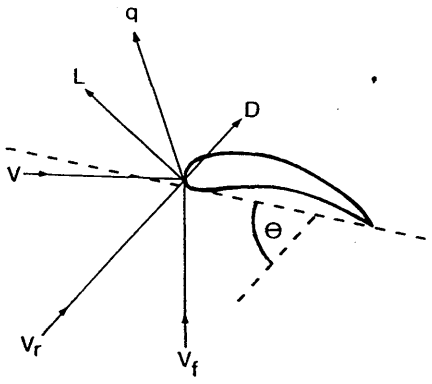


Fig 5.2. Local velocities and forces on the wingtip of a rigid wing (ie one which is not capable of canting forwards). Labels as for Fig 5.1.

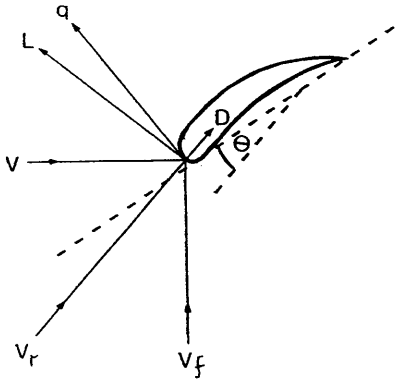


Fig 5.3. Local velocities and forces on a canted wingtip. Labels as for Fig 5.1.

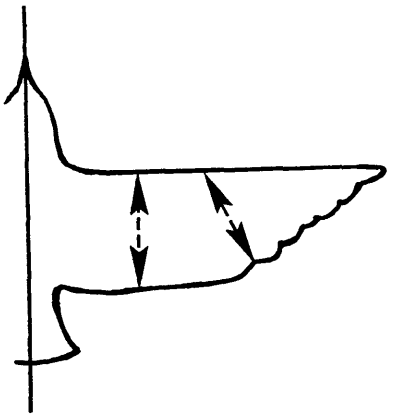


Fig 6.1. Lines along which wing camber was measured.

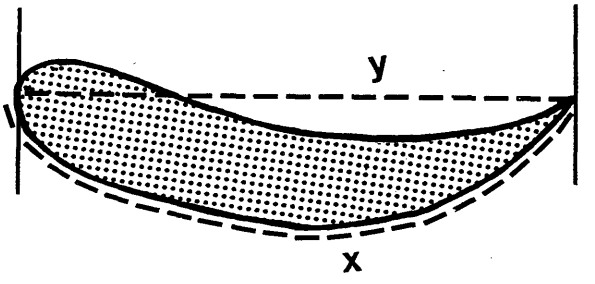


Fig 6.2. Chord-wise cross-section of an idealised wing (leading edge of the wing to the left and ventral surface of wing uppermost). Distances marked x and y were measured as described in the text.

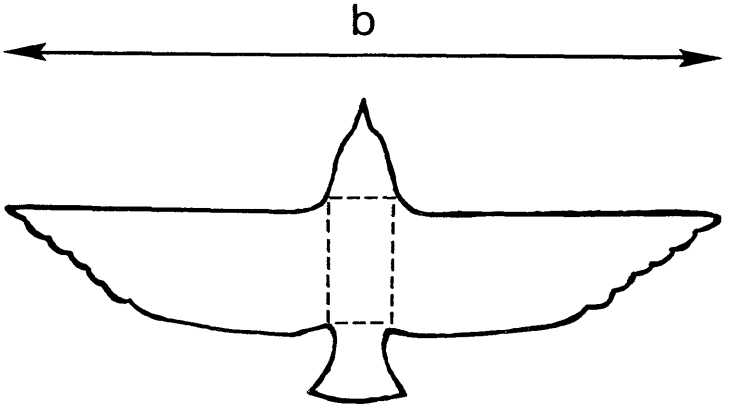


Fig 6.3. Wingspan measured from wingtip to wingtip when wings spread to maximum extent. Planform area includes areas of both wings when spread to the extent shown and the area of the body in between (delimited by the dashed rectangle).

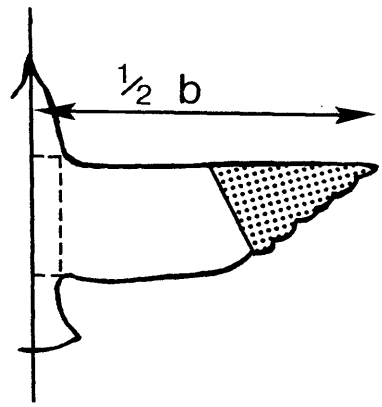


Fig 6.4. Half of the total planform area was determined by tracing the area of one wing spread to maximum extent and extending this area to the body mid-line by measuring the pre-determined distance 1/2 b from the wingtip. The area of the wing as the manus is shaded.

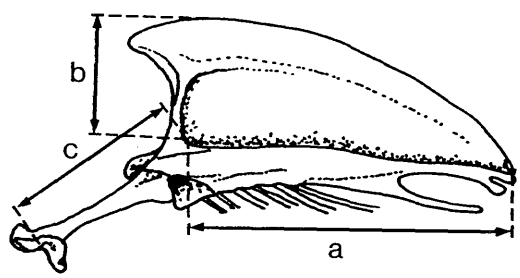


Fig 6.5. Lateral view of sternum. Sternum length (a), keel depth (b), coracoid length (c). After Piersma et al. (1984).

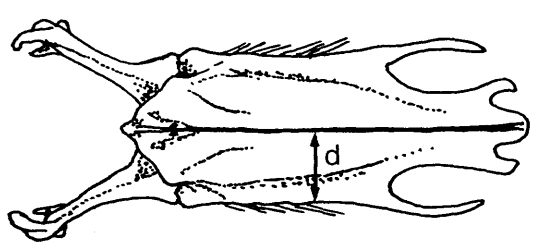


Fig 6.6. Ventral view of sternum. Sternum width (d). After Piersma et al. (1984).

Fig. 6.7 Dorso-ventral deflections under static load applied at distances along the shafts of primary feathers (P10) of Arctic skuas and a common gull.

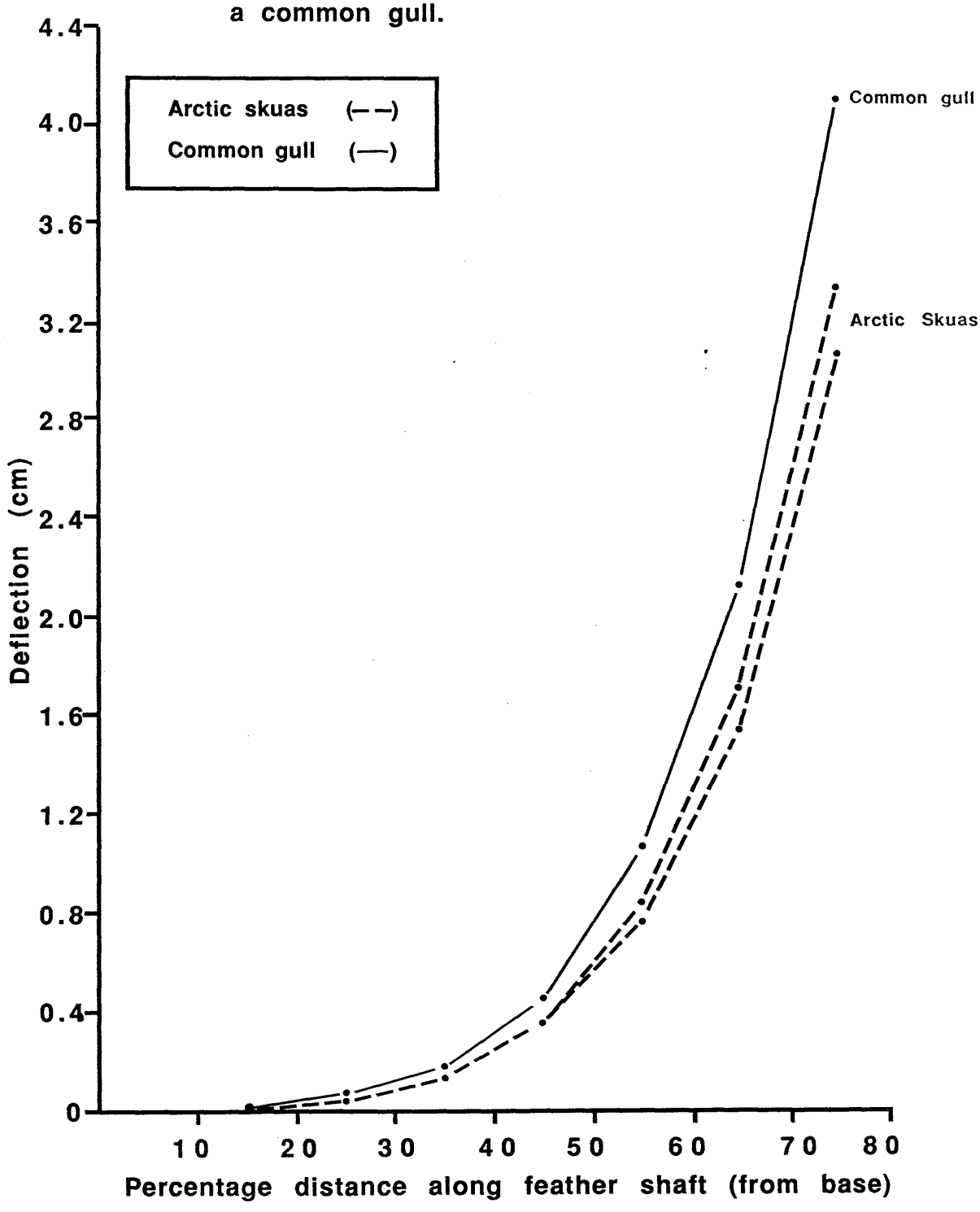


Fig 6.8 Lateral deflections under static load applied at distances along the shafts of primary feathers (P10) of Arctic skuas and a common gull.

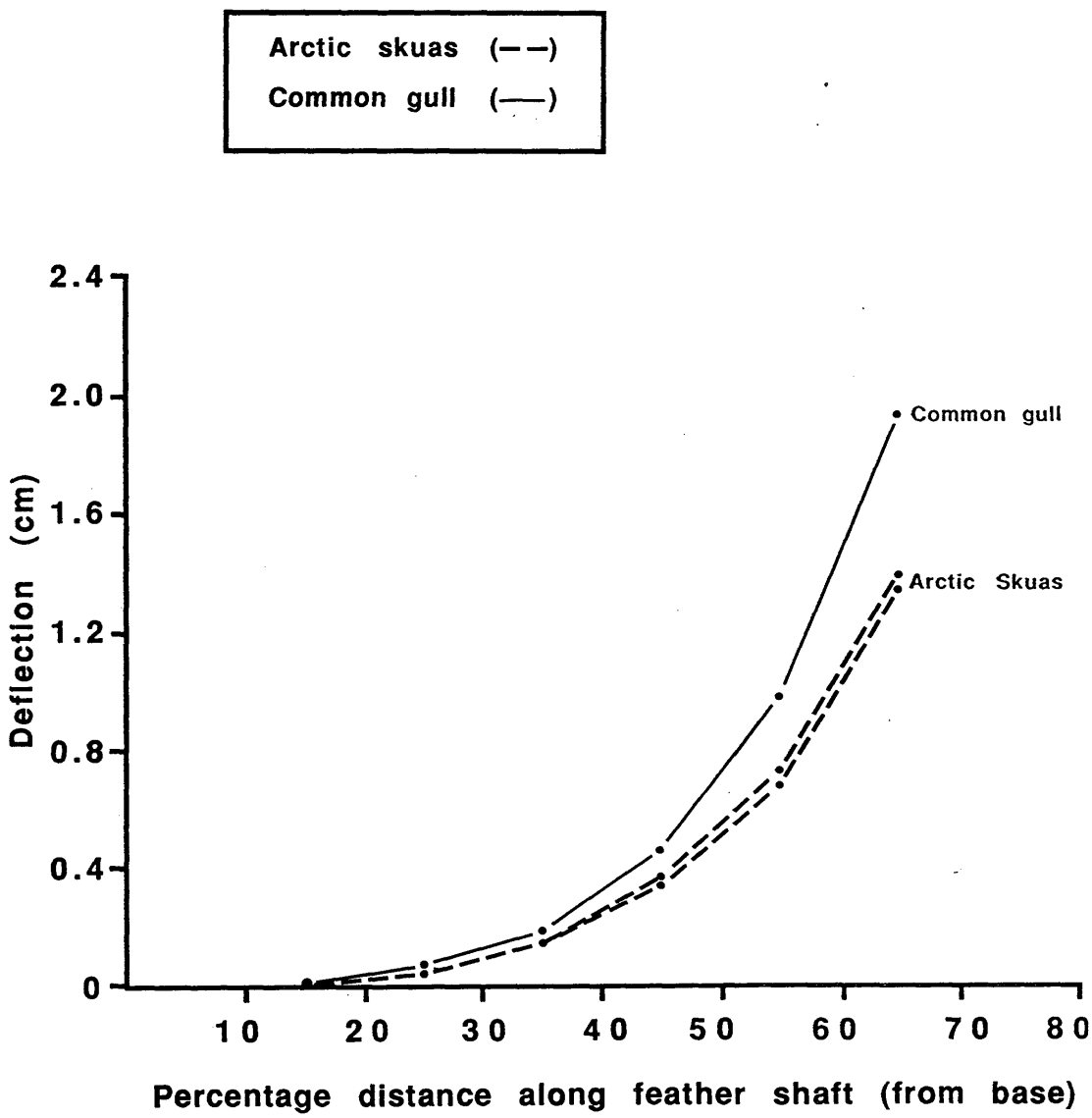


Fig. 6.9 Dorso-ventral deflections under static load applied at distances along the shafts of primary feathers (P9) of Arctic skuas and a common gull.

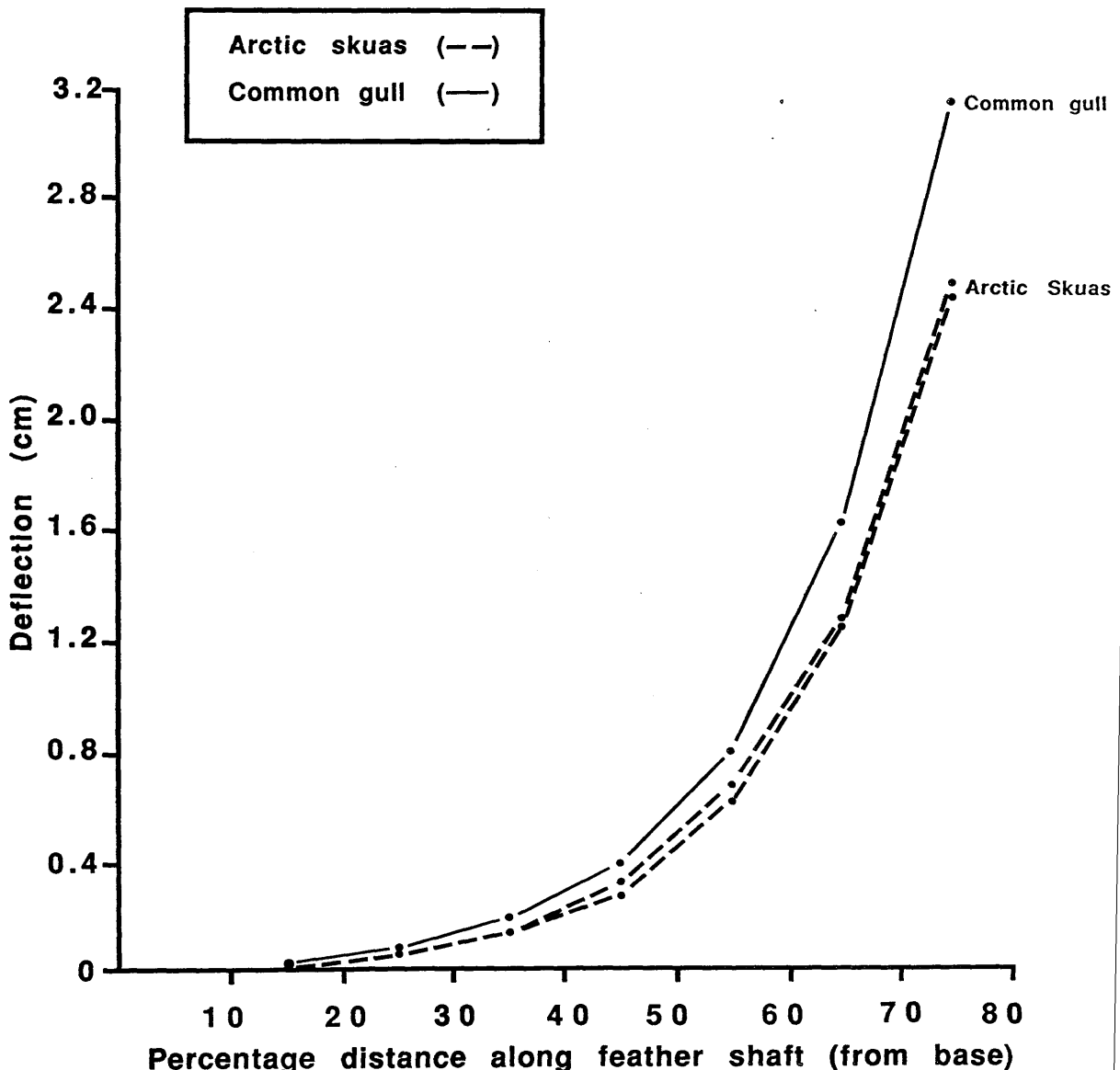


Fig 6.10 Lateral deflections under static load applied at distances along the shafts of primary feathers (P9) of Arctic skuas and a common gull.

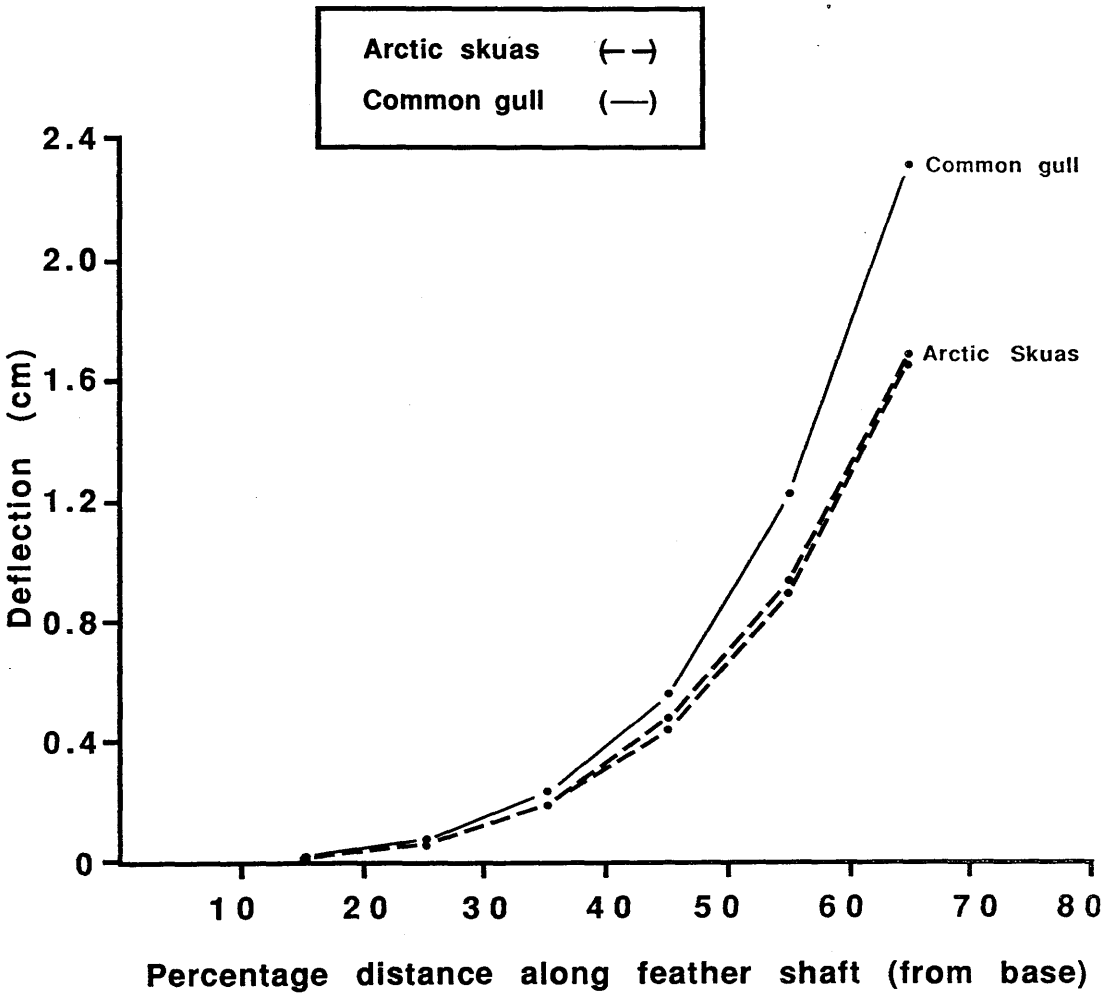


Fig. 6.11 Dorso ventral deflections under static load applied at distances along the shafts of tail feathers (T6) of Arctic skuas and a common gull.

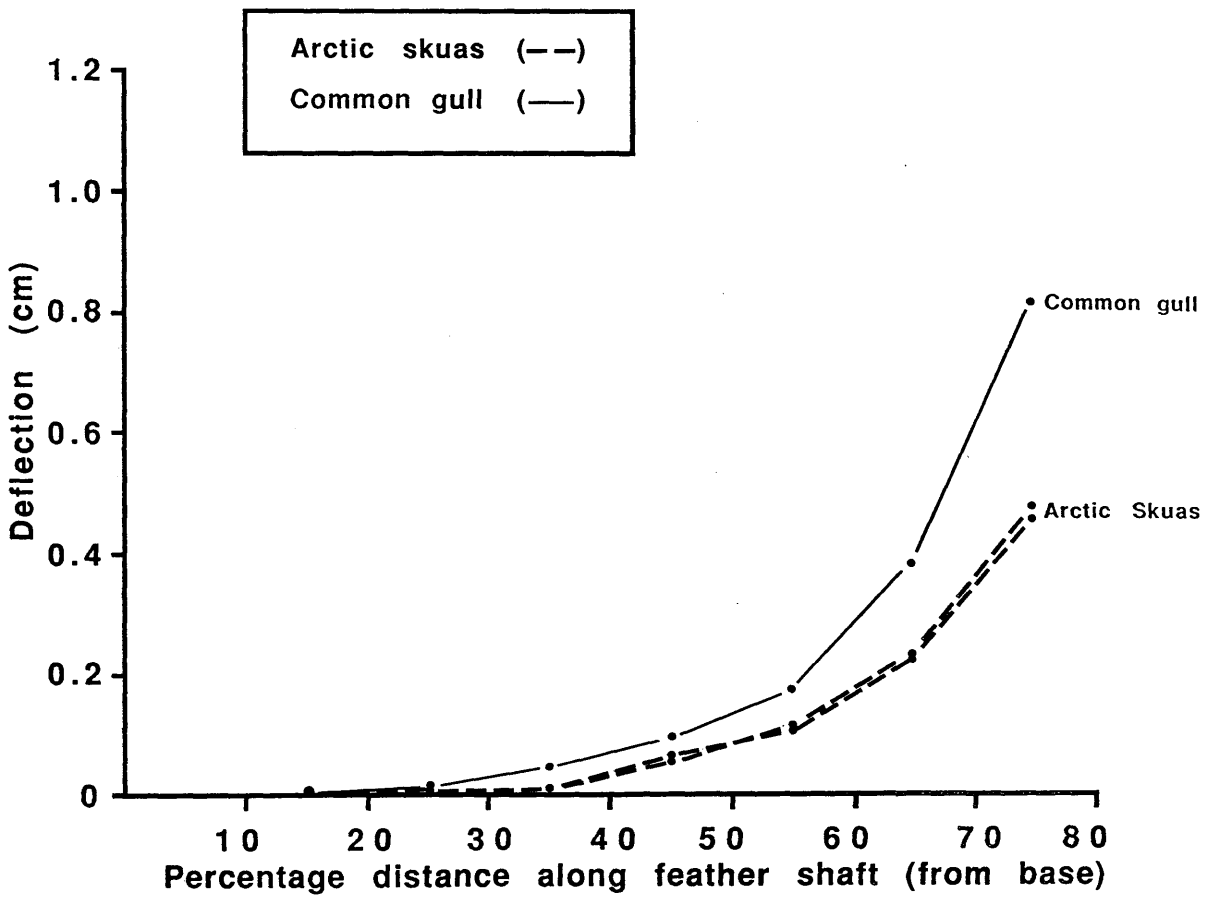


Fig. 6.12 lateral deflections under static load applied at distances along the shafts of tail feathers (T6) of Arctic skuas and a common gull.

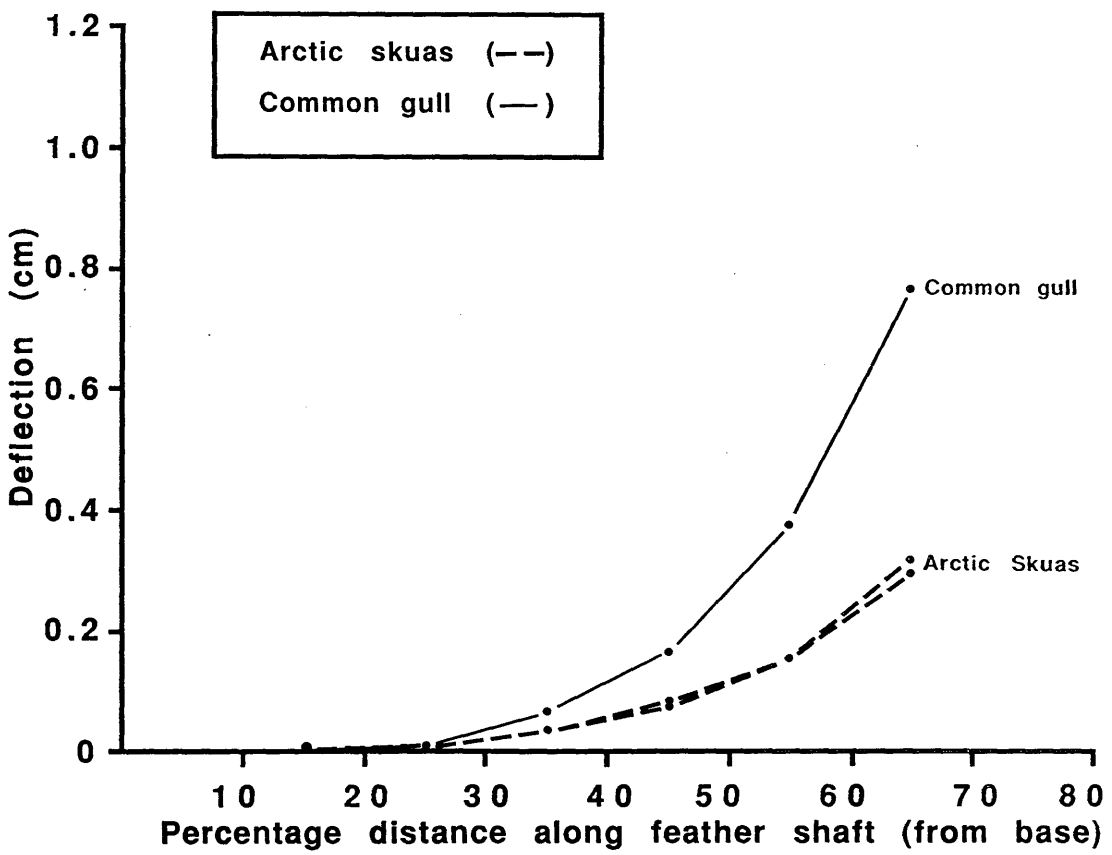


Fig. 6.13 Dorso-ventral deflections under static load applied at distances along the shafts of secondary feathers (S1) of Arctic skuas and a common gull.

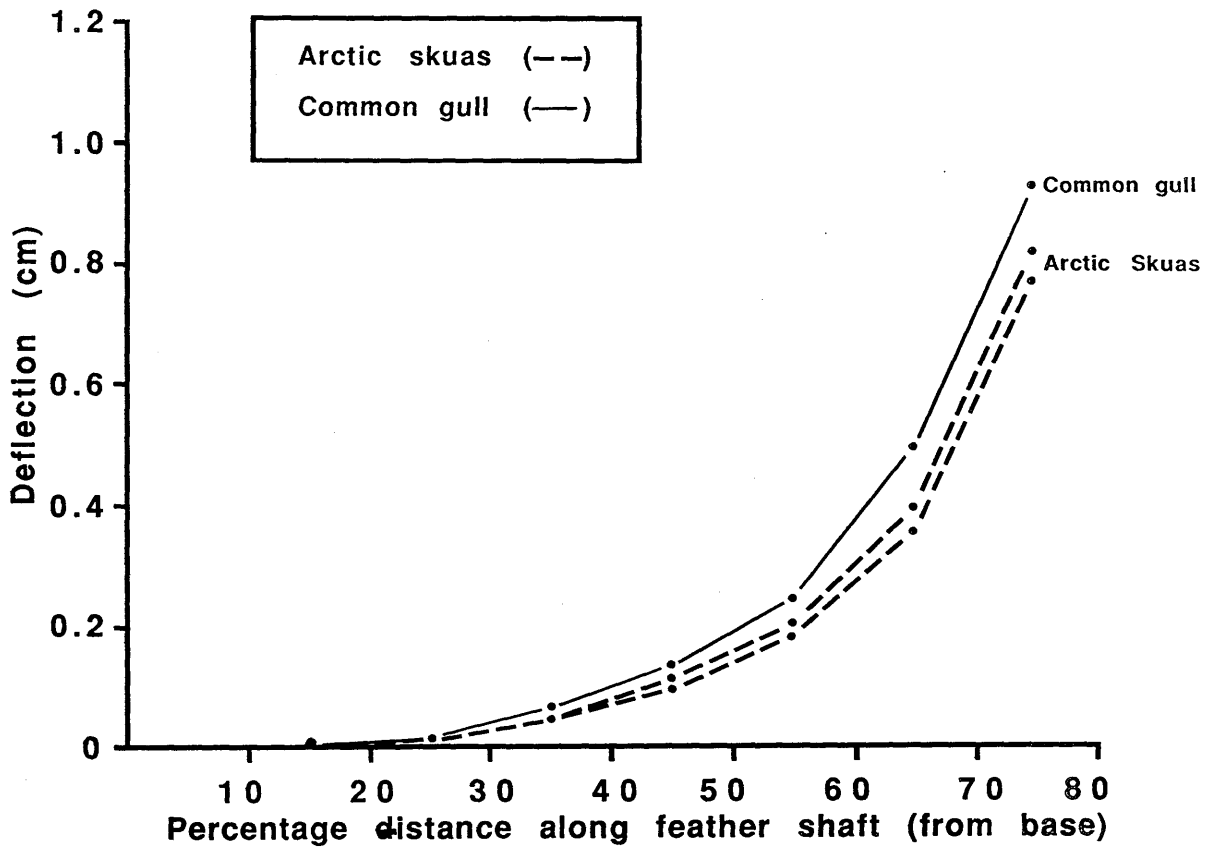


Fig. 6.14 lateral deflections under static load applied at distances along the shafts of secondary feathers (S1) of Arctic skuas and a common gull.

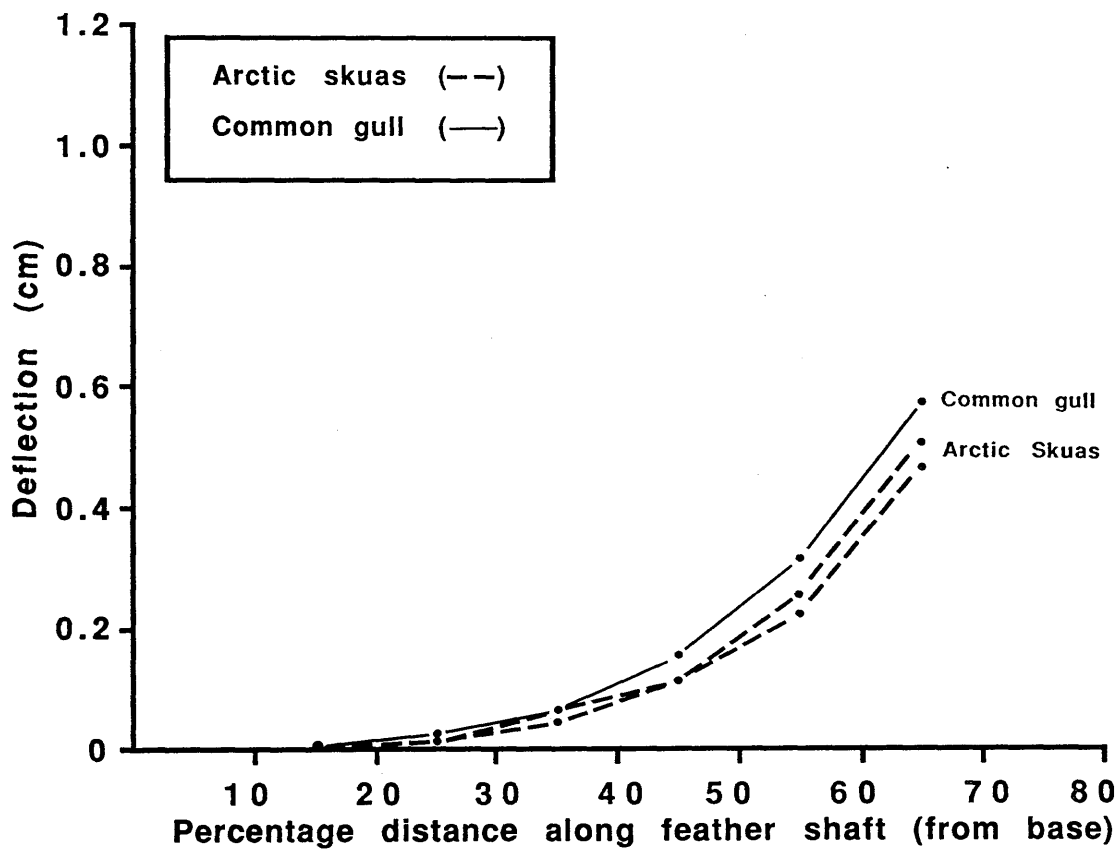


Fig. 6.15 Dorso-ventral deflections under static load applied at distances along the shafts of primary feathers (PI0) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas.

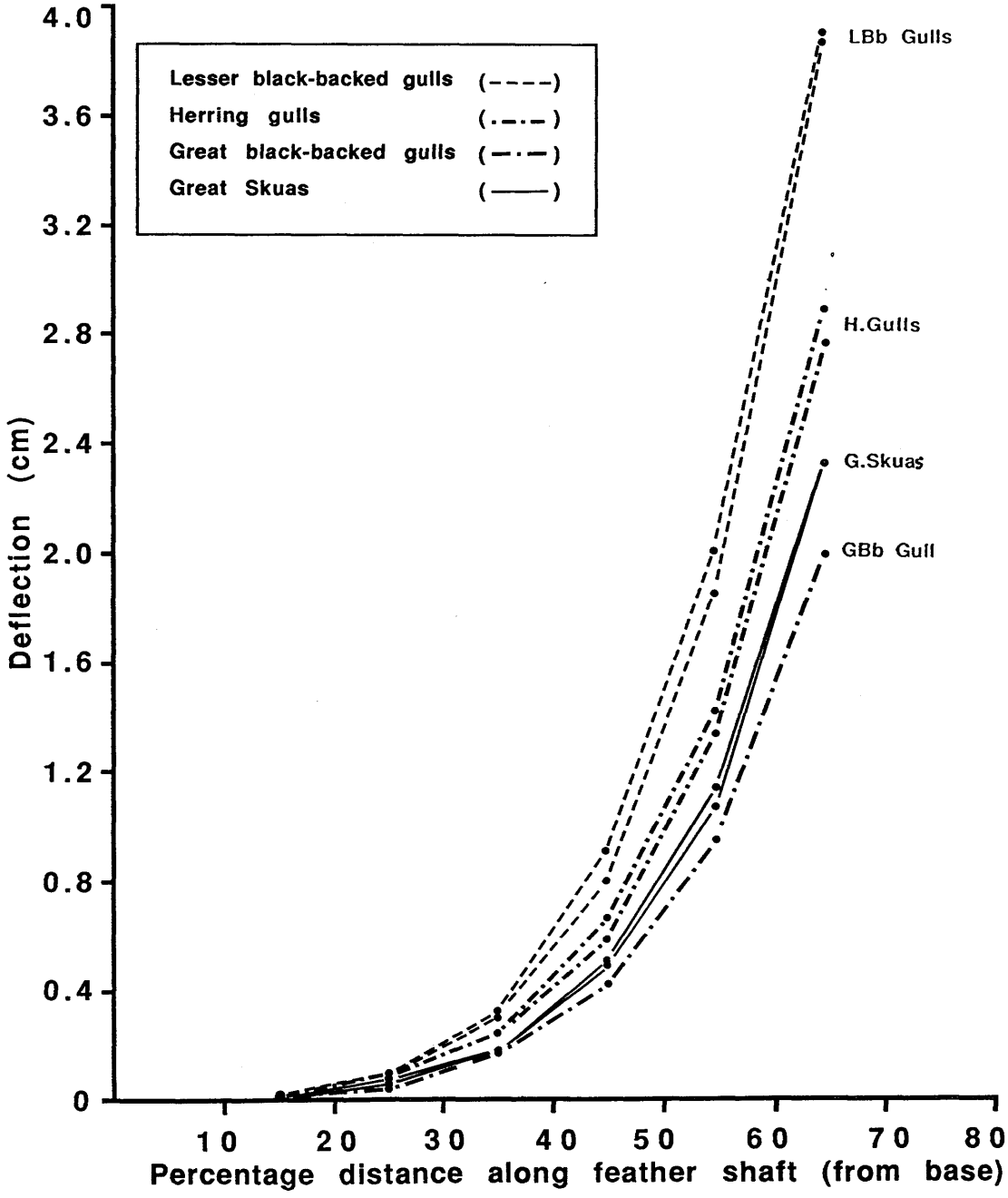


Fig. 6.16 **Lateral deflections under static load applied at distances along the shafts of primary feathers (P10) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas**

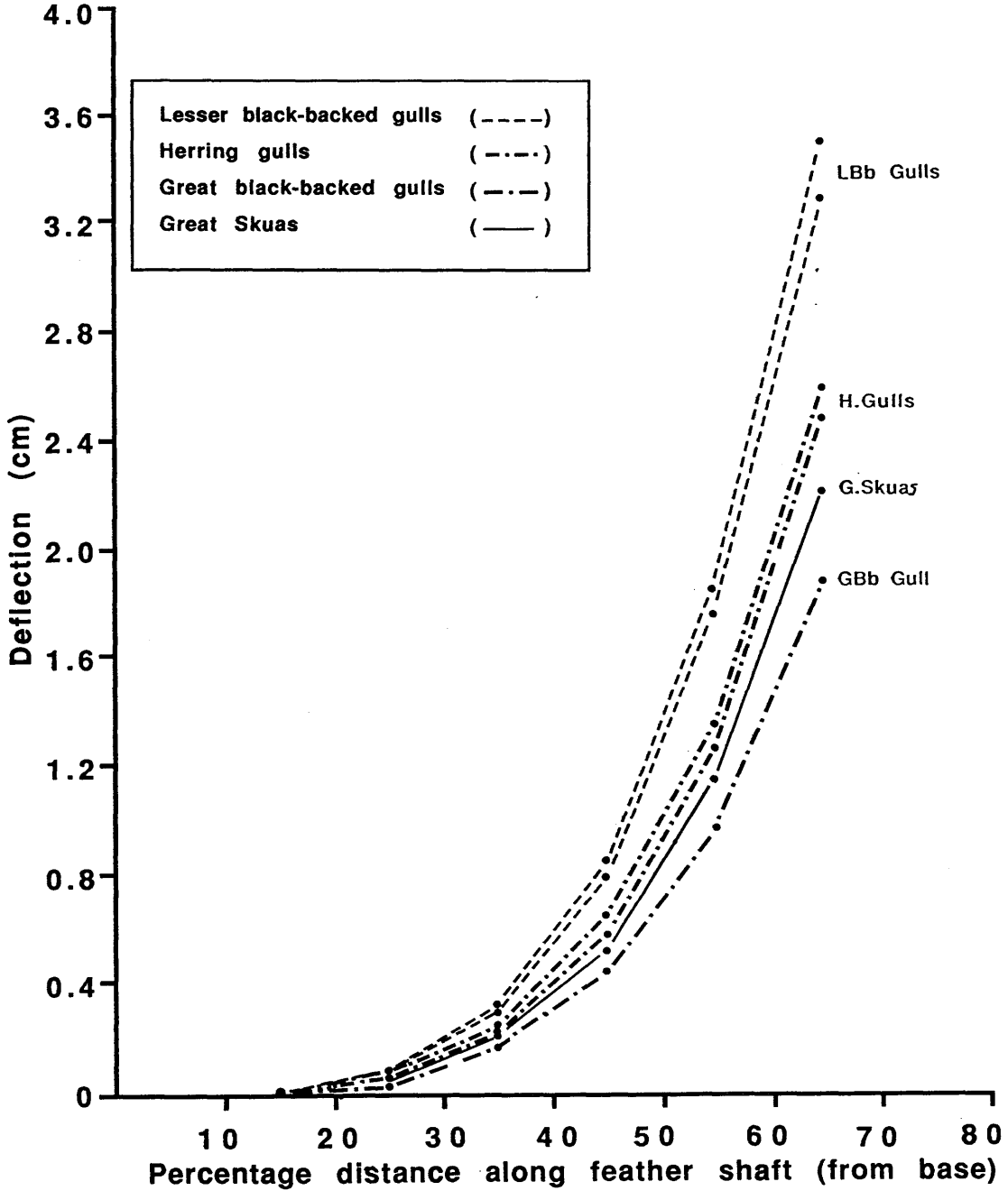


Fig. 6.17 Dorso-ventral deflections under static load applied at distances along the shafts of primary feathers (P9) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas.

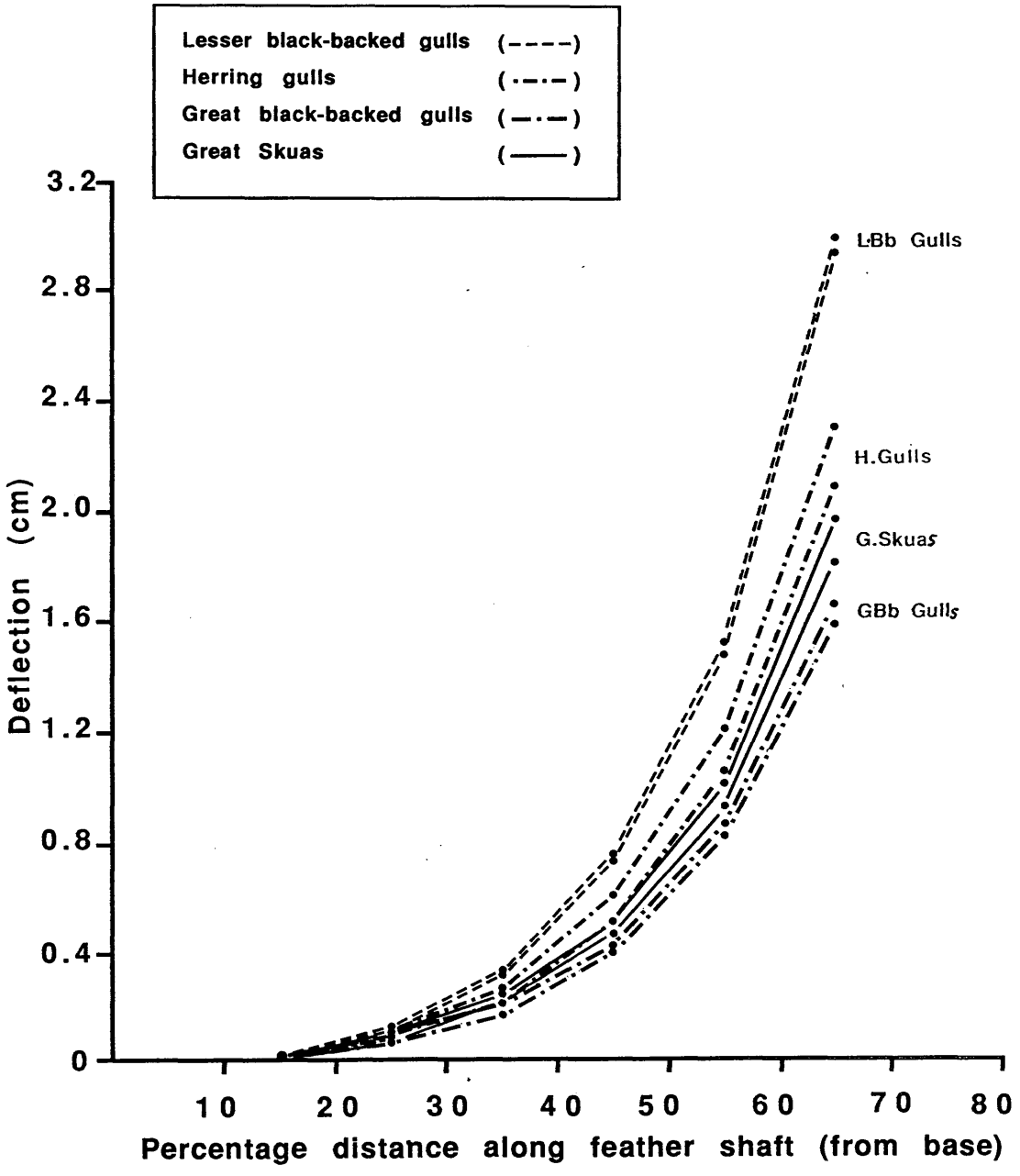


Fig. 6.18 Lateral deflections under static load applied at distances along the shafts of primary feathers (P9) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas.

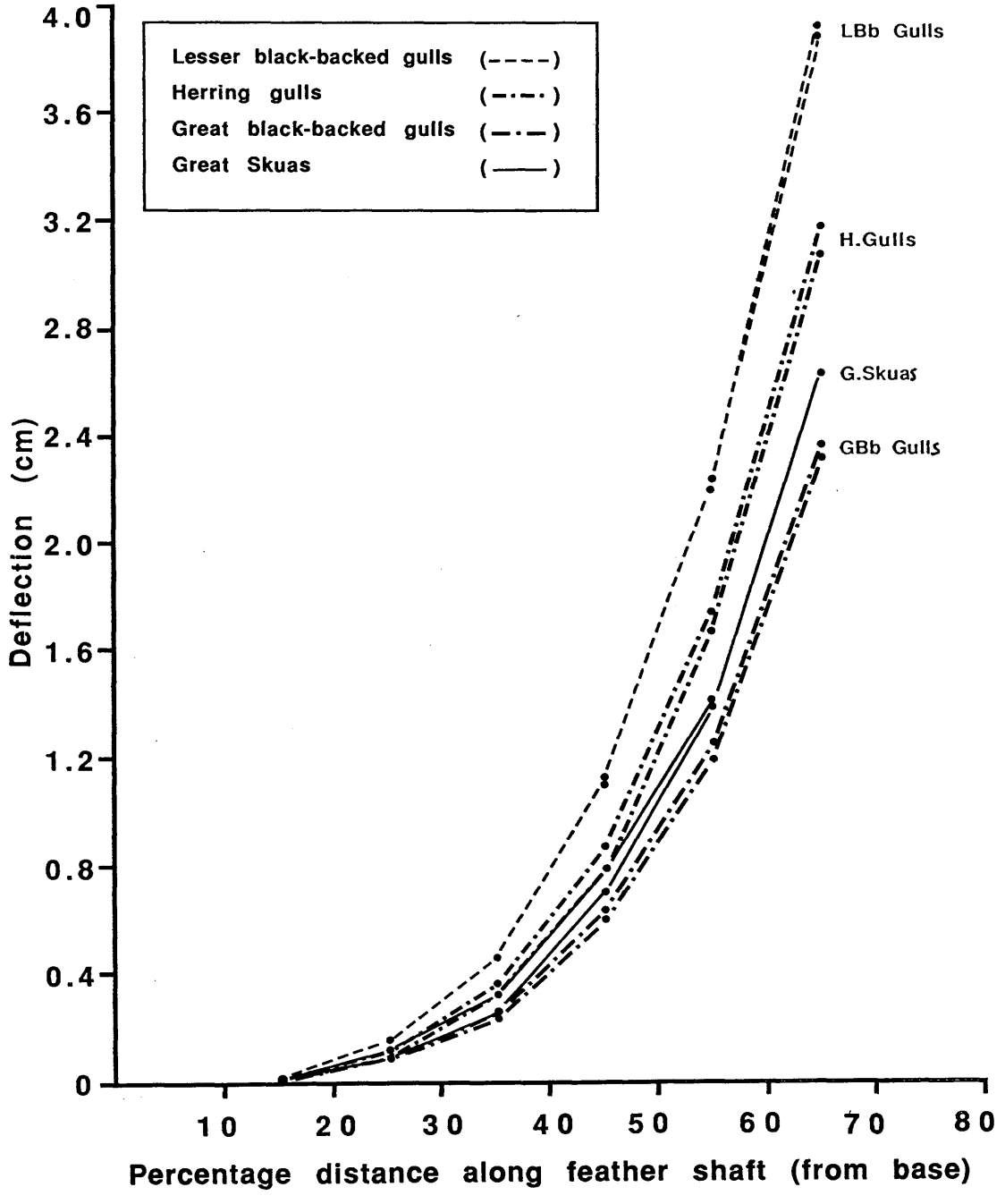


Fig. 6.19 Dorso-ventral deflections under static load applied at distances along the shafts of tail feathers (T6) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas.

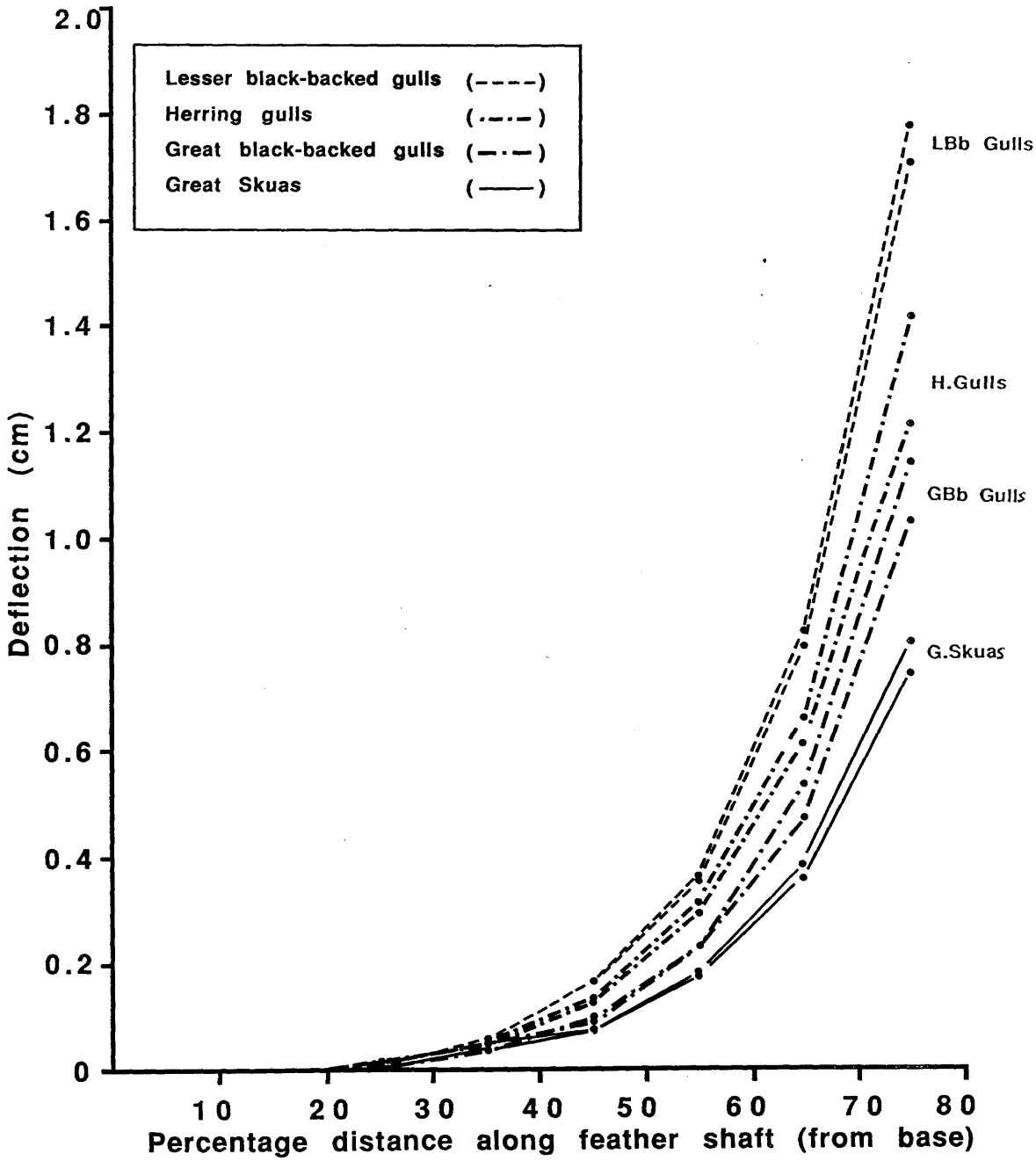


Fig. 6.20 Lateral deflections under static load applied at distances along the shafts of tail feathers (T6) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas.

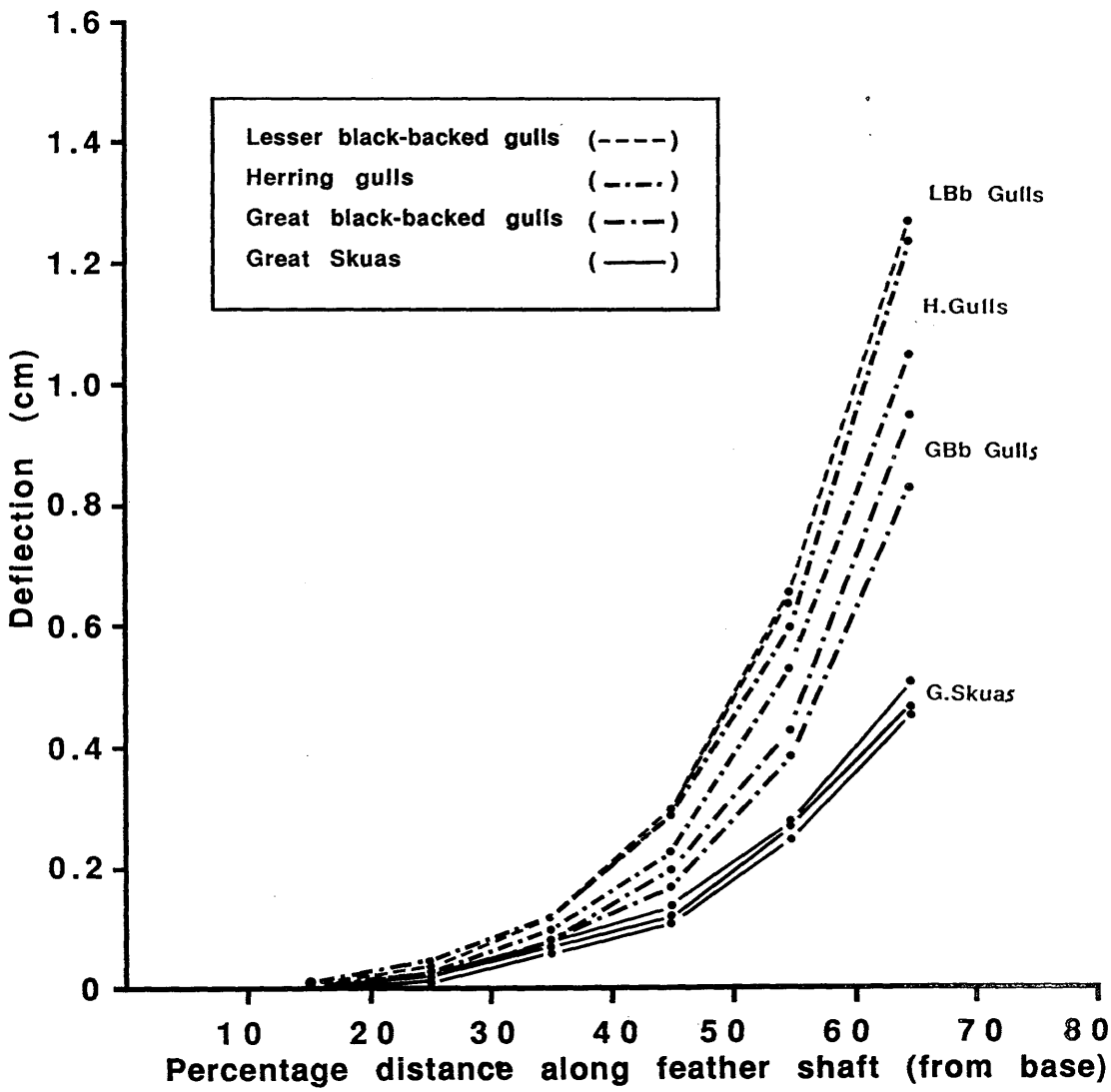


Fig 6.21 Dorso-ventral deflections under static load applied at distances along the shafts of secondary feathers (S2) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas.

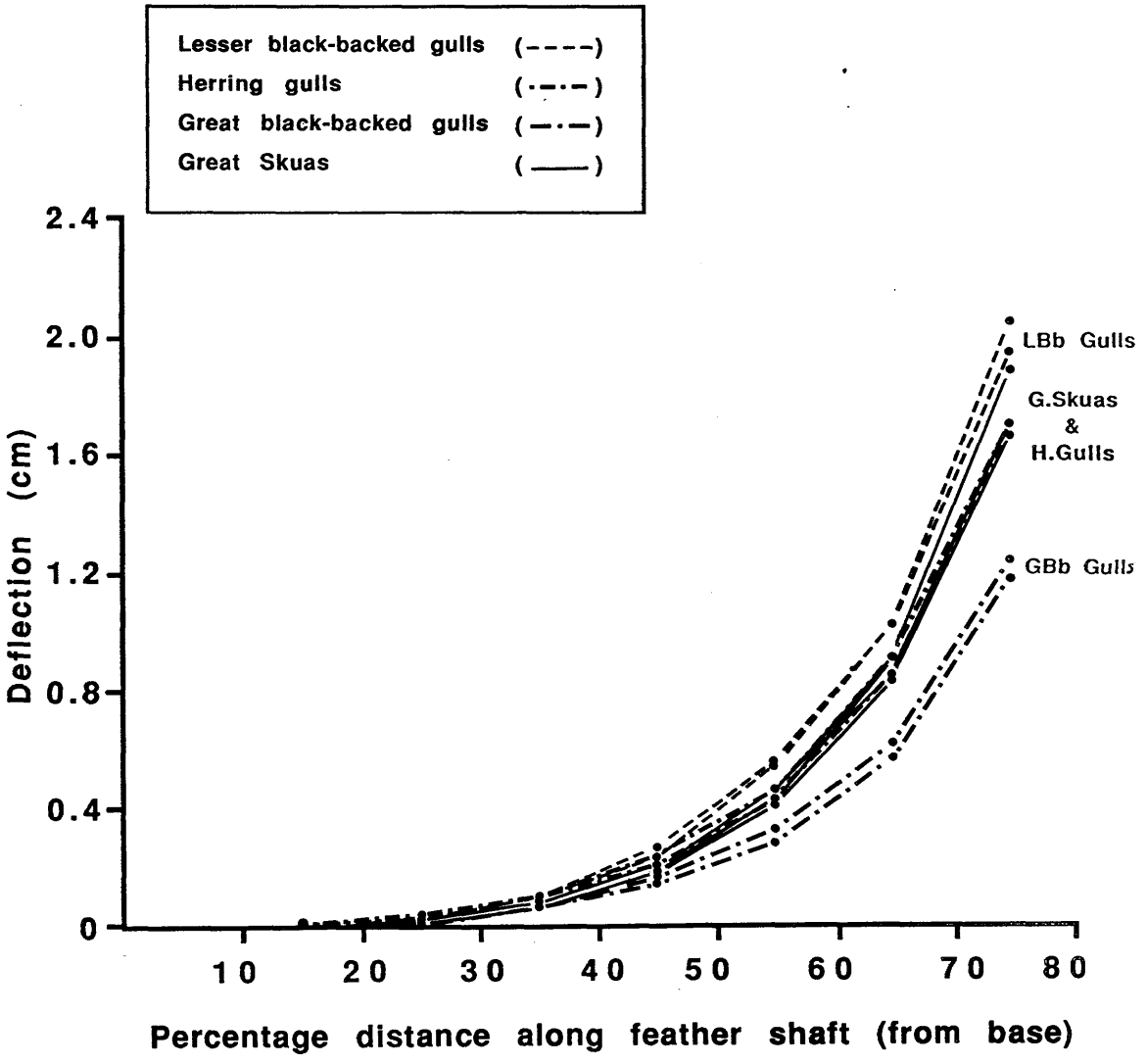


Fig. 6.22 Lateral deflections under static load applied at distances along the shafts of secondary feathers (S2) of lesser black-backed gulls, herring gulls, great black-backed gulls and great skuas.

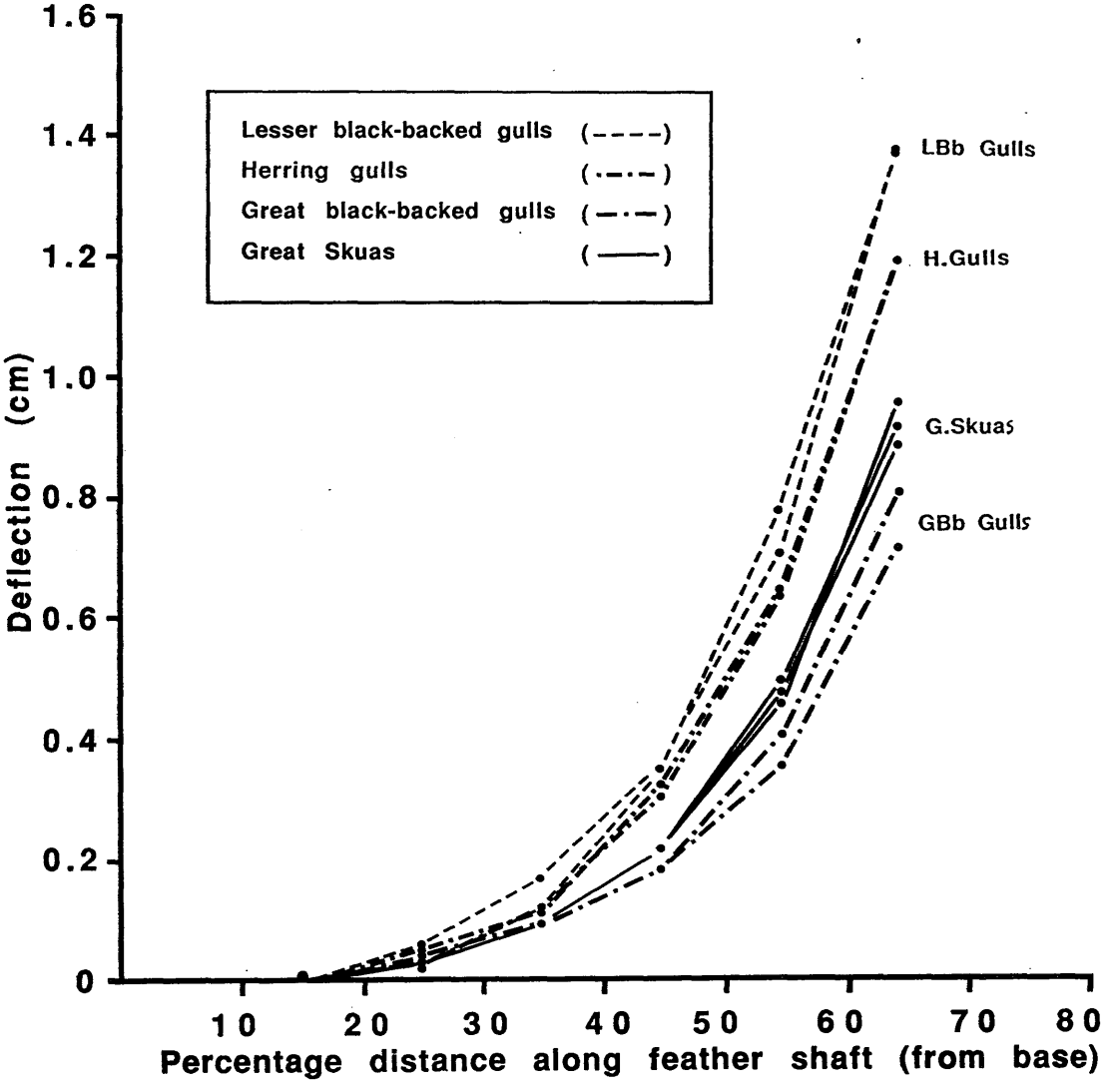
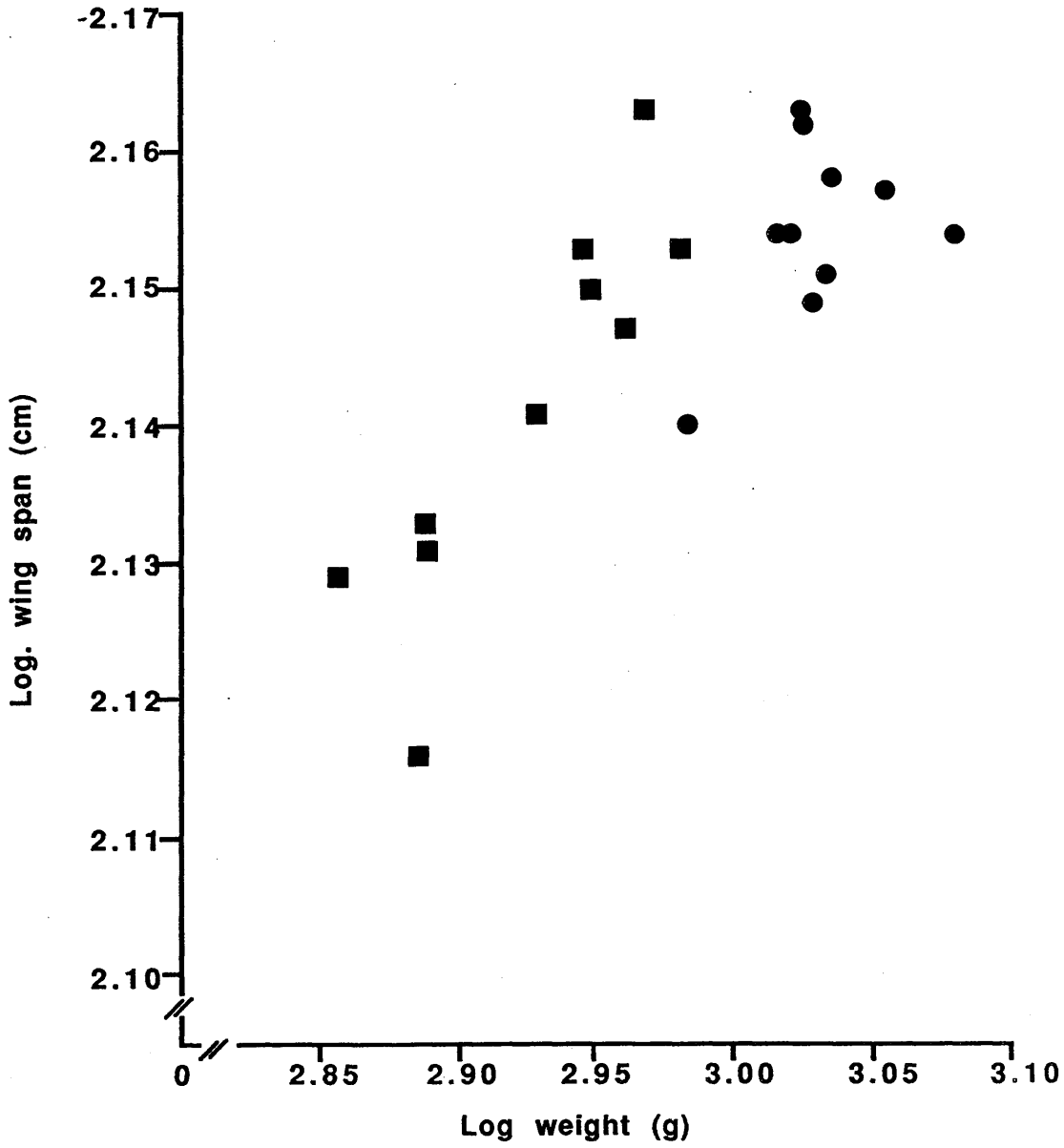


Fig. 6.23 Plot of log wing span against log body weight for herring gulls (●) and lesser black-backed gulls (■).



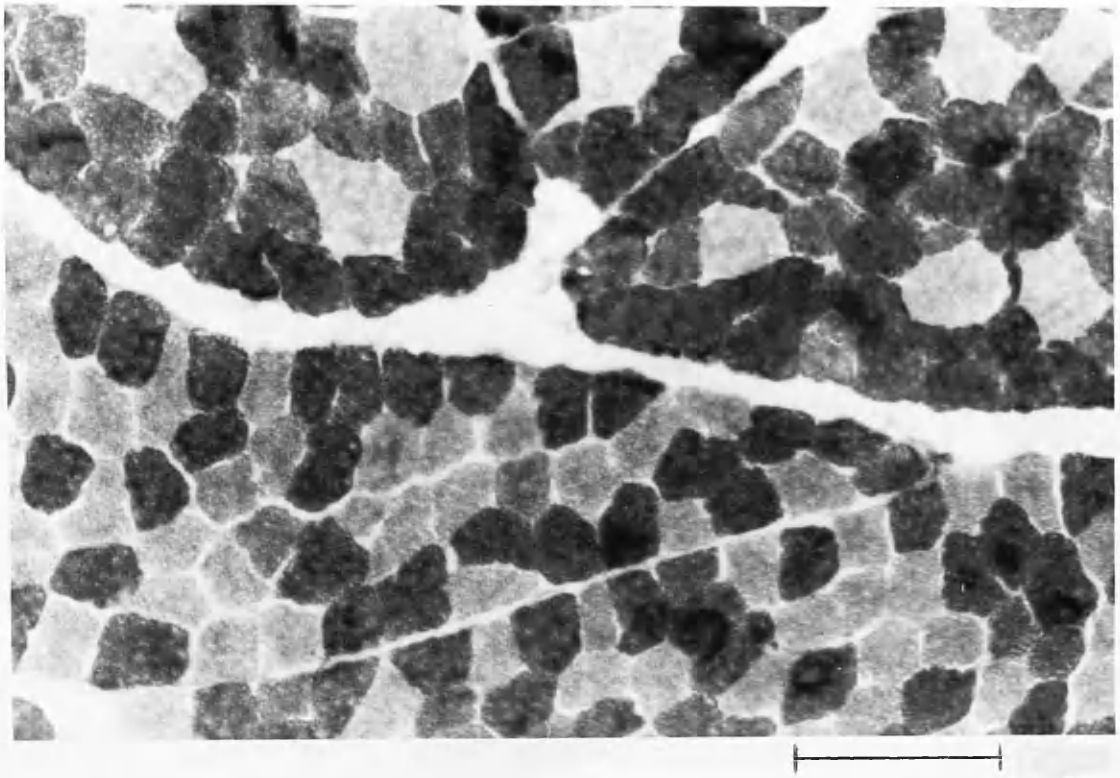


Fig 7.1. Pectoralis major muscle (block PMj1) (lower) and iliofibularis muscle (upper) of herring gull. Section stained for mATPase activity after pre-incubation at pH 10.5. Scale bar = 100 μm.

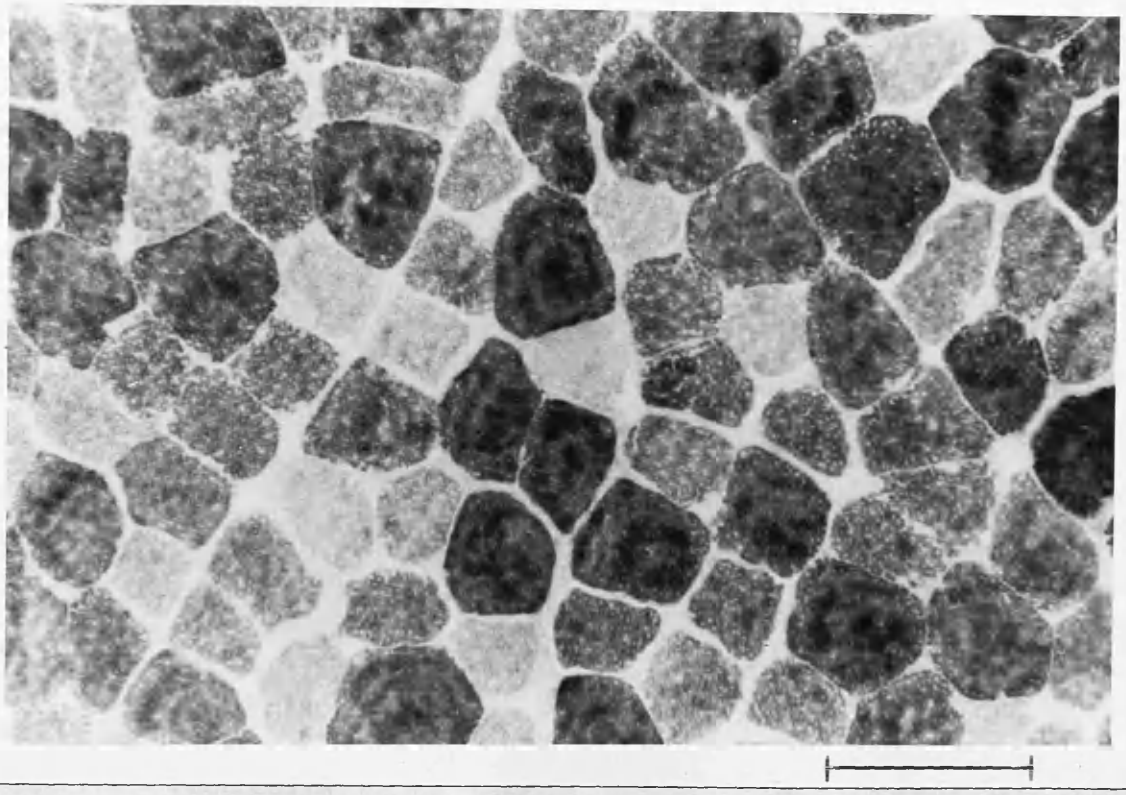


Fig 7.2. Pectoralis minor muscle of herring gull. Section stained for mATPase activity after pre-incubation at pH 10.5. Scale bar = 100 μm.

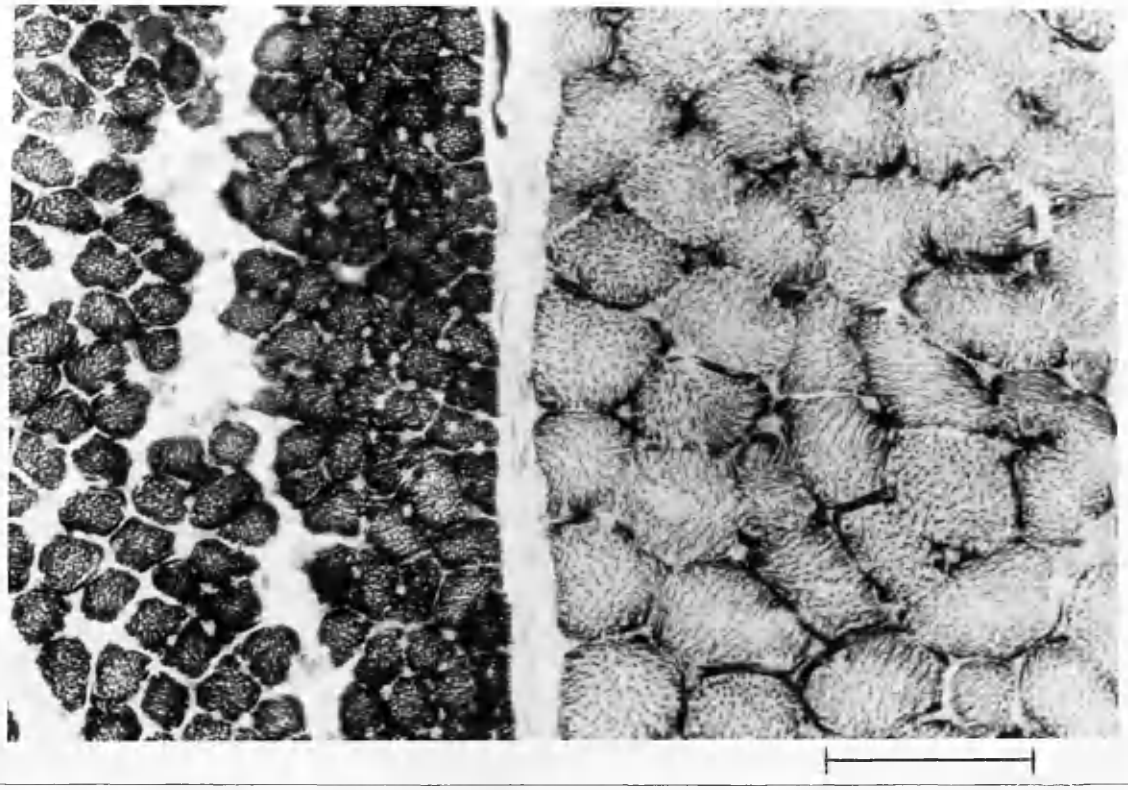


Fig 7.3. Pectoralis major muscle (block PMj1) (left) and iliofibularis muscle (right) of great skua. Section stained for NADH-TR activity. Scale bar = 100 μm.

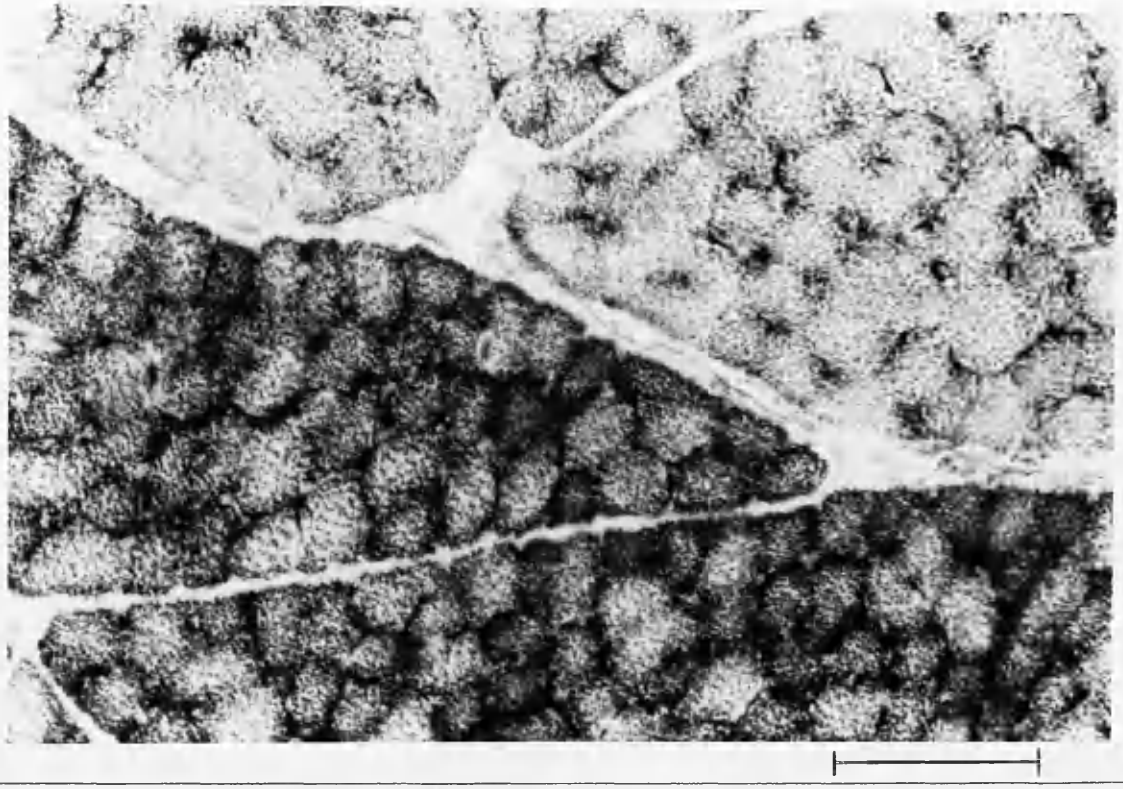


Fig 7.4. Pectoralis major muscle (block PMj1) (lower) and iliofibularis muscle (upper) of herring gull. Section stained for NADH-TR activity. Scale bar = 100 μm.

Table 2.1. Success rates of kleptoparasitic chases by single Arctic skuas of light and melanic phases, 1986 data.

victim		phase of skua: light	phase of skua: melanic	X^2	P
puffin	No chases[1]	252	760		
	No succ[2]	52	145	0.20	0.654
	% succ[3]	20.6	19.1		
guillemot	No chases	33	148		
	No succ	7	16	1.78	0.182
	% succ	21.2	10.8		
razorbill	No chases	26	100		
	No succ	6	11	1.65	0.199
	% succ	23.1	11.0		
black guillemot	No chases	0	1		
	No succ	-	0	-	-
	% succ	-	0.0		
auk	No chases	45	62		
	No succ	3	11	1.92	0.166
	% succ	6.7	17.7		
kittiwake	No chases	1	6		
	No succ	0	0	-	-
	% succ	0.0	0.0		
Arctic skua	No chases	0	2		
	No succ	-	0	-	-
	% succ	-	0.0		
All Species	No chases	357	1079		
	No succ	68	183	0.67	0.412
	% succ	19.0	17.0		

key:
1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.

Table 2.2. Success rates of kleptoparasitic chases by single Arctic skuas of light and melanic phases, 1987 data.

victim		phase of skua: light	phase of skua: melanic	X^2	P
puffin	No chases[1]	98	243	2.11	0.146
	No succ[2]	23	39		
	% succ[3]	23.5	16.0		
guillemot	No chases	21	50	0.87	0.351
	No succ	4	4		
	% succ	19.0	8.0		
razorbill	No chases	12	39	0.00	1.000
	No succ	4	11		
	% succ	33.3	28.2		
auk	No chases	32	81	0.00	1.000
	No succ	3	7		
	% succ	9.4	8.6		
kittiwake	No chases	0	1	-	-
	No succ	-	1		
	% succ	-	100.0		
Arctic tern	No chases	3	2	-	*1.000
	No succ	2	1		
	% succ	66.7	50.0		
All Species	No chases	166	416	3.15	0.076
	No succ	36	63		
	% succ	21.7	15.1		

key:
1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.

*. Fisher's exact test.

Table 2.3. Success rates of kleptoparasitic chases by two or more Arctic skuas, 1986 data.

victim		phase of skua: at least one light	phase of skua: all melanic	X^2	P
puffin	No chases[1]	47	37	0.86	0.353
	No succ[2]	17	9		
	% succ[3]	36.2	24.3		
guillemot	No chases	5	2	-	0.286 *
	No succ	0	1		
	% succ	0.0	50.0		
razorbill	No chases	1	6	-	1.000 *
	No succ	0	1		
	% succ	0.0	16.7		
auk	No chases	0	2	-	-
	No succ	-	1		
	% succ	-	50.0		
All Species	No chases	53	47	0.25	0.618
	No succ	17	12		
	% succ	32.1	25.5		

key:

1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.

*. Fisher's exact tests.

Table 2.4. Success rates of kleptoparasitic chases by two or more Arctic skuas, 1987 data.

victim		phase of skua: at least one light	phase of skua: all melanic	X^2	P
puffin	No chases[1]	13	18	0.00	1.000
	No succ[2]	5	7		
	% succ[3]	38.5	38.9		
guillemot	No chases	2	1	-	-
	No succ	0	0		
	% succ	0.0	0.0		
razorbill	No chases	1	0	-	-
	No succ	0	0		
	% succ	0.0	-		
auk	No chases	1	0	-	-
	No succ	0	0		
	% succ	0.0	-		
kittiwake	No chases	1	1	-	-
	No succ	0	0		
	% succ	0.0	0.0		
Arctic tern	No chases	1	1	-	-
	No succ	1	1		
	% succ	100.0	100.0		
All Species	No chases	19	21	0.01	0.921
	No succ	6	8		
	% succ	31.6	38.1		

key:
1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.

Table 2.5. Success rates of kleptoparasitic chases by single Arctic skuas and groups of more than one Arctic skua, 1986 data.

victim		number of skuas: one[1]	number of skuas: more than one[1]	X^2	P
puffin	No chases[2]	1027	84	5.51	0.019
	No succ[3]	201	26		
	% succ[4]	19.6	31.0		
guillemot	No chases	189	7	0.00	1.000
	No succ	23	1		
	% succ	12.2	14.3		
razorbill	No chases	132	7	0.00	1.000
	No succ	17	1		
	% succ	12.9	14.3		
black guillemot	No chases	1	0	-	-
	No succ	0	-		
	% succ	0.0	-		
auk	No chases	114	2	0.26	0.608
	No succ	14	1		
	% succ	12.3	50.0		
kittiwake	No chases	7	0	-	-
	No succ	0	-		
	% succ	0.0	-		
Arctic skua	No chases	2	0	-	-
	No succ	0	-		
	% succ	0.0	-		
All Species	No chases	1472	100	7.85	0.005
	No succ	255	29		
	% succ	17.3	29.0		

key:

1. Includes chases in which the phase of the attackers were not recorded.
2. Total number of chases of known outcome recorded.
3. Number of successful chases recorded.
4. Percentage of the total number of chases, of known outcome, that were successful.

Table 2.6. Success rates of kleptoparasitic chases by single Arctic skuas and groups of more than one Arctic skua, 1987 data.

victim		number of skuas: one[1]	number of skuas: more than one[1]	X^2	P
puffin	No chases[2]	373	31	7.63	0.006
	No succ[3]	63	12		
	% succ[4]	16.9	38.7		
guillemot	No chases	86	3	0.00	1.000
	No succ	10	0		
	% succ	11.6	0.0		
razorbill	No chases	60	1	0.00	1.000
	No succ	15	0		
	% succ	25.0	0.0		
auk	No chases	135	1	0.00	1.000
	No succ	13	0		
	% succ	9.6	0.0		
kittiwake	No chases	2	2	-	*1.000
	No succ	1	0		
	% succ	50.0	0.0		
Arctic tern	No chases	8	2	-	*0.467
	No succ	4	2		
	% succ	50.0	100.0		
All Species	No chases	664	40	8.37	0.004
	No succ	106	14		
	% succ	16.0	35.0		

key:

1. Includes chases in which the phases of the attackers were not recorded.
2. Total number of chases of known outcome recorded.
3. Number of successful chases recorded.
4. Percentage of the total number of chases, of known outcome, that were successful.

*. Fisher's exact test.

Table 2.7. Success rates of kleptoparasitic chases by single great skuas and groups of more than one great skua, 1986 data.

victim		number of skuas one	more than one	X^2	P
	N° chases[1]	302	26		
puffin	N° succ[2]	77	8	0.13	0.722
	% succ[3]	25.5	30.8		
	N° chases	258	9		
guillemot	N° succ	51	1	0.05	0.829
	% succ	19.8	11.1		
	N° chases	36	0		
razorbill	N° succ	10	-	-	-
	% succ	27.8	-		
	N° chases	176	6		
auk	N° succ	44	2	0.00	1.000
	% succ	25.0	33.3		
	N° chases	22	5		
gannet	N° succ	3	0	-	-
	% succ	13.6	0.0		
	N° chases	1	1		
kittiwake	N° succ	0	0	-	-
	% succ	0.0	0.0		
	N° chases	3	0		
Arctic	N° succ	1	-	-	-
skua	% succ	33.3	-		
	N° chases	2	0		
shag	N° succ	0	-	-	-
	% succ	0.0	-		
great	N° chases	1	0		
black-backed	N° succ	0	-	-	-
gull	% succ	0.0	-		
	N° chases	801	47		
All	N° succ	186	11	0.00	1.000
Species	% succ	23.2	23.4		

key: 1. Total number of chases of known outcome recorded. 2. Number of successful chases recorded. 3. Percentage of the total number of chases, of known outcome, that were successful.

Table 2.8. Success rates of kleptoparasitic chases by single great skuas and groups of more than one great skua, 1987 data.

victim		number of skuas: one	number of skuas: more than one	X^2	P
puffin	No chases[1]	83	9	0.00	1.000
	No succ[2]	28	3		
	% succ[3]	33.7	33.3		
guillemot	No chases	89	5	2.60	0.107
	No succ	17	3		
	% succ	19.1	60.0		
razorbill	No chases	12	0	-	-
	No succ	2	-		
	% succ	16.7	-		
auk	No chases	66	4	0.00	1.000
	No succ	26	2		
	% succ	39.4	50.0		
gannet	No chases	27	0	-	-
	No succ	5	-		
	% succ	18.5	-		
kittiwake	No chases	1	1	-	-
	No succ	0	0		
	% succ	0.0	0.0		
great skua	No chases	2	1	-	*1.000
	No succ	1	0		
	% succ	50.0	0.0		
great black-backed gull	No chases	2	0	-	-
	No succ	0	-		
	% succ	0.0	-		
All Species	No chases	283	20	0.81	0.369
	No succ	79	8		
	% succ	27.9	40.0		

key: 1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.
*. Fisher's exact test.

Table 2.9. Success rates of kleptoparasitic chases by single great skuas and Arctic skuas, 1986 data.

	species of skua							
	great skua			Arctic skua				
victim	No of[1] chases	No[2] succ	% [3] succ	No of[4] chases	No succ	% succ	X^2	P
puffin	302	77	25.5	1027	201	19.6	4.60	0.032
guillemot	258	51	19.8	189	23	12.2	4.03	0.045
razorbill	36	10	27.8	132	17	12.9	3.62	0.057
black guillemot	0	-	-	1	0	0.0	-	-
auk	176	44	25.0	114	14	12.3	6.22	0.013
gannet	22	3	13.6	0	-	-	-	-
kittiwake	1	0	0.0	7	0	0.0	-	-
Arctic skua	3	1	33.3	2	0	0.0	-	*1.000
shag	2	0	0.0	0	-	-	-	-
great black-backed gull	1	0	0.0	0	-	-	-	-
All Species	801	186	23.2	1472	255	17.3	11.16	<0.001

key:
1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.
4. Includes chases in which the phase of the attacker was not recorded.

*. Fisher's exact test.

Table 2.10. Success rates of kleptoparasitic chases by single great skuas and Arctic skuas, 1987 data.

	species of skua							
	great skua			Arctic skua				
victim	No of[1] chases	No[2] succ	% [3] succ	No of[4] chases	No succ	% succ	X^2	P
puffin	83	28	33.7	373	63	16.9	11.03	<0.001
guillemot	89	17	19.1	86	10	11.6	1.34	0.247
razorbill	12	2	16.7	60	15	25.0	0.06	0.804
auk	66	26	39.4	135	13	9.6	23.25	<0.001
gannet	27	5	18.5	0	-	-	-	-
kittiwake	1	0	0.0	2	1	50.0	-	*1.000
great skua	2	1	50.0	0	-	-	-	-
great black-backed gull	2	0	0.0	0	-	-	-	-
Arctic tern	0	-	-	8	4	50.0	-	-
All Species	283	79	27.9	664	106	16.0	17.28	<0.001

key:
1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.
4. Includes chases in which the phase of the attackers were not recorded.

*. Fisher's exact test.

Table 2.11. Success rates of kleptoparasitic chases by groups of more than one great skua and groups of more than one Arctic skua, 1986 data.

	species of skua							
	great skuas			Arctic skuas				
victim	No of[1] chases	No[2] succ	% [3] succ	No of[4] chases	No succ	% succ	X^2	P
puffin	26	8	30.8	84	26	31.0	0.00	1.000
guillemot	9	1	11.1	7	1	14.3	-	*1.000
razorbill	0	-	-	7	1	14.3	-	-
auk	6	2	33.3	2	1	50.0	-	*1.000
gannet	5	0	0.0	0	-	-	-	-
kittiwake	1	0	0.0	0	-	-	-	-
All Species	47	11	23.4	100	29	29.0	0.26	0.609

key:
1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.
4. Includes chases in which the phases of the attackers were not recorded.

*. Fisher's exact test.

Table 2.12. Success rates of kleptoparasitic chases by groups of more than one great skua and groups of more than one Arctic skua, 1987 data.

	species of skua							
	great skuas			Arctic skuas				
victim	No of[1] chases	No[2] succ	% 3 succ	No of[4] chases	No succ	% succ	X^2	P
puffin	9	3	33.3	31	12	38.7	0.00	1.000
guillemot	5	3	60.0	3	0	0.0	-	*0.196
razorbill	0	-	-	1	0	0.0	-	-
auk	4	2	50.0	1	0	0.0	-	*1.000
kittiwake	1	0	0.0	2	0	0.0	-	-
great skua	1	0	0.0	0	-	-	-	-
Arctic tern	0	-	-	2	2	100.0	-	-
All species	20	8	40.0	40	14	35.0	0.01	0.925

key:
1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of the total number of chases, of known outcome, that were successful.
4. Includes chases in which the phase of the attackers were not recorded.

*. Fisher's exact test.

Table 2.13. Success rates of single Arctic skuas, great skuas and gulls recorded in 1986, 1987 and 1988.

year		1986	1987	1988	Total
Arctic skuas					
All victims	No chases[1]	1472	664	664	2800
	No succ[2]	255	106	108	469
	% succ[3]	17.3	16.0	16.3	16.8
puffins	No chases	1027	373	555	1955
	No succ	201	63	100	364
	% succ	19.6	16.9	18.0	18.6
great skuas					
All victims	No chases	801	283	-	1084
	No succ	186	79	-	265
	% succ	23.2	27.9	-	24.4
puffins	No chases	302	83	-	385
	No succ	77	28	-	105
	% succ	25.5	33.7	-	27.3
gulls					
All victims	No chases	17	4	27	48
	No succ	3	0	0	3
	% succ	17.6	0.0	0.0	6.3
puffins	No chases	9	1	25	35
	No succ	3	0	0	3
	% succ	33.3	0.0	0.0	8.6

key:

1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of total number of chases, of known outcome, that were successful.

Table 2.14. Success rates of single light phase and melanic phase Arctic skuas against puffins and guillemots in 1978, 1979, 1986 and 1987. Data for 1978 and 1979 from Furness (1980).

year		1978	1979	1986	1987
Light phase Arctic skuas					
puffins	No chases[1]	52	123	252	98
	No succ[2]	8	25	52	23
	% succ[3]	15.4	20.3	20.6	23.5
guillemots	No chases	12	6	33	21
	No succ	2	2	7	4
	% succ	16.7	33.3	21.2	19.0
Melanic phase Arctic skuas					
puffins	No chases	88	163	760	243
	No succ	22	46	145	39
	% succ	25.0	28.2	19.1	16.0
guillemots	No chases	14	29	148	50
	No succ	0	6	16	4
	% succ	0.0	20.7	10.8	8.0

key:

1. Total number of chases of known outcome recorded.
2. Number of successful chases recorded.
3. Percentage of total number of chases, of known outcome, that were successful.

Table 2.15. Success rates of attackers and initiators in securing fish in relation to numbers of attackers.

		Arctic skuas		great skuas	
number of attackers		one	two	one	two
1986	No chases[1]	1470	88	794	39
	No any attacker succ[2]	169	17	129	3
	% any attacker succ[3]	11.5	19.3	16.2	7.7
	No chases[4]	1470	86	794	38
	No initiator succ[5]	169	10	129	2
	% initiator succ[6]	11.5	11.6	16.2	5.3
1987	No chases[1]	671	36	288	19
	No any attacker succ[2]	74	9	61	5
	% any attacker succ[3]	11.0	25.0	21.2	26.3
	No chases[4]	671	31	288	16
	No initiator succ[5]	74	3	61	1
	% initiator succ[6]	11.0	9.7	21.2	6.3

key:

1 Total number of chases of known outcome.
2. Total number of chases in which an attacker secured fish.
3. Total number of chases in which an attacker secured fish, expressed as a percentage of the total number of chases of known outcome.
4. Total number of chases in which it is known which, if any, attacker secured fish.
5. Total number of chases in which the chase initiator secured fish.
6. Total number of chases in which the chase initiator secured fish, expressed as a percentage of the total number of chases in which it is known which, if any, attacker secured fish.

For chases by groups of two skuas, the numbers of chases in category 4 are lower than the numbers in category 1 because in some cases it was uncertain which of the two attackers was successful.

Table 2.16. Success rates of Arctic skuas and great skuas in securing fish from their three main host species.

victim		puffin	guillemot	razorbill
Arctic skuas				
	N° chases[1]	1108	196	139
1986	N° succ[2]	155	18	11
	% succ[3]	14.0	9.2	7.9
	N° chases	411	90	61
1987	N° succ	52	9	8
	% succ	12.7	10.0	13.1
great skuas				
	N° chases	323	267	36
1986	N° succ	61	32	6
	% succ	18.9	12.0	16.7
	N° chases	94	96	12
1987	N° succ	26	13	2
	% succ	27.7	13.5	16.7

key:

1. Total number of chases of known outcome with respect to attackers.
2. Total number of chases in which attackers secured fish.
3. Total number of chases in which attackers secured fish, expressed as a percentage of the total number of chases of known outcome with respect to attackers.

Table 2.17. Indices of host availability to Arctic skuas and great skuas and their host selection patterns.

		host species		
		puffin	guillemot	razorbill
1986 Arctic skuas	Index of availability *	767	103	138
	Host selection pattern **	1123	143	134
great skuas	Index of availability	128	461	33
	Host selection pattern	324	265	35
1987 Arctic skuas	Index of availability	373	147	149
	Host selection pattern	417	62	59
great skuas	Index of availability	99	511	62
	Host selection pattern	100	97	12

key:

*. Values are the total number of each species seen arriving with fish during one hour observation periods over the whole season. Totals for great skuas and Arctic skuas differ because of the spatial segregation of their feeding areas.

**. Values are the total number of chases of each species of victim recorded throughout the whole season at the location in question.

Table 2.18. Success rates of Arctic skuas and great skuas against various species of host since 1975. Data for 1975-76 from Furness (1978a). Data for 1978-80 from Furness (1980).

		year					
		1975-76	1978	1979	1980	1986	1987
Arctic skuas							
	No chases[1]	110	144	289	250	1111	404
puffins	No succ[2]	23	32	74	77	227	75
	% succ[3]	20.9	22.2	25.6	30.8	20.4	18.6
	No chases	27	26	36	41	196	89
guillemots	No succ	3	2	8	9	24	10
	% succ	11.1	7.7	22.2	22.0	12.2	11.2
	No chases	18	0	0	0	139	61
razorbills	No succ	2	-	-	-	18	15
	% succ	11.1	-	-	-	12.9	24.6
	No chases	87	17	374	23	0	10
Arctic terns	No succ	38	1	91	4	-	6
	% succ	43.7	5.9	24.3	17.4	-	60.0
great skuas							
	No chases	223	-	-	-	328	92
puffins	No succ	84	-	-	-	85	31
	% succ	37.7	-	-	-	25.9	33.7
	No chases	113	-	-	-	267	94
guillemots	No succ	33	-	-	-	52	20
	% succ	29.2	-	-	-	19.5	21.3
	No chases	38	-	-	-	36	12
razorbills	No succ	7	-	-	-	10	2
	% succ	18.4	-	-	-	27.7	16.7
	No chases	69	-	-	-	27	27
gannets	No succ	21	-	-	-	3	5
	% succ	30.4	-	-	-	11.1	18.5

key:

1. Total number of chases of known outcome with respect to victims.
2. Total number of chases in which victim lost fish.
3. Percentage of total number of chases, of known outcome with respect to the victim, in which victim lost fish.

Table 2.19. Number of chases of the main host species by Arctic skuas and great skuas since 1975. Data for 1975-76 from Furness (1978a). Data for 1978 and 1979 from Furness (1980).

		year				
	site*	1975-76	1978	1979	1986	1987
Arctic skuas						
puffins	1	14	150	292	-	417
guillemots	1	0	27	36	-	62
razorbills	1	3	0	4	-	59
kittiwakes	1	13	4	30	-	5
Arctic terns	1	87	17	379	-	8
great skuas						
puffins	2	217	-	-	324	100
guillemots	2	113	-	-	265	97
razorbills	2	31	-	-	35	12
kittiwakes	2	11	-	-	4	4
gannets	2	69	-	-	28	26

key:

*. 1 = Heddlicliff, 2 = Kittiwakes' Haa.

Table 2.20. Methods of, and efficiency at securing fish from all victims and from puffins only. Data for 1986.

		attacker			
		Arctic skua light	Arctic skua melanic	Arctic skua all phases	great skua
		NO	NO	NO	NO
How victims lost fish					
	dropped	42	101	146	146
All victims	stolen from bill	18	49	68	3
	lost on impact	3	13	16	13
	dropped	29	78	110	65
puffins	stolen from bill	18	46	65	1
	lost on impact	3	10	13	5
Ability to secure dropped fish					
	secured	23	41	66	95
All victims	not secured	19	60	80	45
	secured	16	29	47	45
puffins	not secured	13	49	63	16
Ability to secure fish from sea					
	secured	19	55	75	102
All victims	not secured	9	32	41	49
	secured	16	38	55	47
puffins	not secured	5	23	28	15
Where skuas secured dropped fish					
	in the air	9	4	13	19
All victims	from the sea	14	37	52	75
	in the air	4	4	8	8
puffins	from the sea	12	25	38	37

Table 2.21. Methods of, and efficiency at securing fish from all victims and from puffins only. Data for 1987.

		attacker			
		Arctic skua light	Arctic skua melanic	Arctic skua all phases	great skua
		NO	NO	NO	NO
How victims lost fish					
All victims	dropped	15	34	52	47
	stolen from bill	15	10	25	1
	lost on impact	2	2	4	3
puffins	dropped	8	21	29	20
	stolen from bill	11	9	20	0
	lost on impact	2	1	3	0
Ability to secure dropped fish					
All victims	secured	7	16	24	32
	not secured	8	18	28	13
puffins	secured	2	9	11	16
	not secured	6	12	18	4
Ability to secure fish from sea					
All victims	secured	4	21	30	52
	not secured	6	10	18	14
puffins	secured	2	13	16	22
	not secured	4	3	7	3
Where skuas secured dropped fish					
All victims	in the air	6	9	15	8
	from the sea	1	6	8	24
puffins	in the air	2	4	6	2
	from the sea	0	5	5	14

Table 2.22. Number of chases in which Arctic skuas and great skuas either secured or failed to secure dropped fish in the air.

year	victim	attacker: Arctic skuas	attacker: great skuas
1986	All species		
	Fish secured in air	13	19
	Fish missed in air	133	127
1986	puffins		
	Fish secured in air	8	8
	Fish missed in air	102	57
1987	All species		
	Fish secured in air	15	8
	Fish missed in air	37	39
1987	puffins		
	Fish secured in air	6	2
	Fish missed in air	23	18

Table 2.23. Number of chases in which Arctic skuas and great skuas either secured or failed to secure fish that had landed on the rocks or on the sea surface.

year	victim	attacker: Arctic skuas	attacker: great skuas
1986	All species		
	Fish secured on the rocks	1	0
	Fish not secured on the rocks	41	1
	Fish secured from the sea	52	76
	Fish not secured from the sea	36	44
1986	puffins		
	Fish secured on the rocks	1	0
	Fish not secured on the rocks	36	1
	Fish secured from the sea	38	38
	Fish not secured from the sea	25	15
1987	All species		
	Fish secured on the rocks	0	0
	Fish not secured on the rocks	11	1
	Fish secured from the sea	9	25
	Fish not secured from the sea	14	12
1987	puffins		
	Fish secured on rocks	0	0
	Fish not secured on rocks	10	1
	Fish secured from the sea	6	14
	Fish not secured from the sea	5	3

Table 2.24. Factors which have a significant influence on the success of all chases and chases of puffins by great skuas and Arctic skuas.

species of skua	victim	independent variable	change in Rao's V	P
great skua	All sp	Speed of reaction (1-3)	9.33	0.002
		Victim's initial height (1-3)	8.91	0.003
		Average visibility (1-4)	4.06	0.044
great skua	puffin	Victim's initial height (1-3)	7.62	0.006
Arctic skua	All sp	Minimum distance (1-2)	14.73	<0.001
		Chase direction,towards (0-1)	6.82	0.009
		Victim's initial height (1-3)	4.13	0.042
		Attacker's initial vertical direction (1-3)	6.55	0.011
Arctic skua	puffin	Minimum distance (1-2)	13.33	<0.001
		Chase direction,towards (0-1)	11.98	<0.001
		Attacker's initial vertical direction (1-3)	5.35	0.021
		Victim's initial height (1-3)	5.27	0.022
		Stage in season (1-10)	5.63	0.018

Table 2.25. The effect of various recorded parameters on success of chases of all victims by great skuas.

variable		categories			X^2	p
		Fast	Intermediate	Slow		
Speed of reaction	succ	23	21	61	28.35	<0.001
	unsucc	148	95	104		
		Above	Same height	Below		
Attacker's height relative to victim's	succ	125	1	2	0.79	0.674
	unsucc	454	9	7		
		Infront	Side	Behind		
Attacker's position relative to victim's	succ	6	2	35	1.61	0.448
	unsucc	15	15	113		
		High	Moderate	Low		
Victim's initial height	succ	41	5	29	9.51	0.009
	unsucc	108	15	173		
		Far	Moderate	Near		
Victim's initial distance from cliff	succ	11	4	17	0.21	0.902
	unsucc	45	21	68		
		Descending	Level	Ascending		
Attacker's initial vertical direction	succ	129	2	1	0.46	0.794
	unsucc	480	12	5		
		<5secs	5-10secs	10-15secs	>15secs	
Chase duration	succ	45	39	11	3	0.40	0.939
	unsucc	194	167	38	11		
		2-4km	4-10km	10-30km	30-60km	
Average visibility	succ	32	28	84	42	0.60	0.896
	unsucc	96	92	273	154		
		contact	no contact			
Contact between victim and attacker	succ	25	125		18.28	<0.001
	unsucc	31	523			

continued/

Table 2.25. continued.

variable		categories		X^2	p
		< 1m	> 1m		
Minimum distance	succ	57	86	19.90	<0.001
	unsucc	116	430		
		flapping	no flapping		
Use of flapping by attacker	succ	71	41	2.52	0.112
	unsucc	232	194		
		swoop down	no swoop down		
Use of swoop down by attacker	succ	73	51	0.80	0.371
	unsucc	257	220		
		turn	no turn		
Use of turns by attacker	succ	12	113	0.79	0.375
	unsucc	32	441		
		towards	not towards		
Chase direction	succ	40	61	0.00	1.000
	unsucc	139	207		
		parallel	not parallel		
Chase direction	succ	14	87	0.87	0.352
	unsucc	64	282		
		away	not away		
Chase direction	succ	50	51	2.76	0.097
	unsucc	137	209		
Date				9.71	0.375

Table 2.26. The effect of various recorded parameters on success of chases of puffins by great skuas.

variable		categories			X^2	p
		Fast	Intermediate	Slow		
Speed of reaction	succ	13	12	19	9.63	0.008
	unsucc	60	53	28		
		Above	Same height	Below		
Attacker's height relative to victim's	succ	50	0	2	1.77	0.412
	unsucc	168	6	7		
		Infront	Side	Behind		
Attacker's position relative to victim's	succ	2	2	15	0.19	0.909
	unsucc	7	8	43		
		High	Moderate	Low		
Victim's initial height	succ	29	4	8	10.54	0.005
	unsucc	70	9	72		
		Far	Moderate	Near		
Victim's initial distance from cliff	succ	6	4	13	0.05	0.973
	unsucc	23	13	48		
		Descending	Level	Ascending		
Attacker's initial vertical direction	succ	55	1	1	0.93	0.628
	unsucc	176	8	5		
		<5secs	5-10secs	10-15secs	>15secs	
Chase duration	succ	18	16	6	2	0.40	0.940
	unsucc	64	65	20	5		
		2-4km	4-10km	10-30km	30-60km	
Average visibility	succ	14	8	34	21	1.56	0.669
	unsucc	32	28	91	74		
		contact	no contact			
Contact between victim and attacker	succ	5	61		1.45	0.229
	unsucc	7	212			

continued/

Table 2.26. continued.

variable		categories		X^2	p
Minimum ** distance	succ	15	47	0.63	0.429
	unsucc	40	175		
Use of flapping by attacker		flapping	no flapping		
	succ	36	21	0.42	0.515
	unsucc	104	78		
Use of swoop down by attacker		swoop down	no swoop down		
	succ	29	24	1.23	0.267
	unsucc	83	102		
Use of turns by attacker		turn	no turn		
	succ	6	48	1.28	0.257
	unsucc	10	172		
Chase direction		towards	not towards		
	succ	10	41	1.67	0.196
	unsucc	15	121		
Chase direction		parallel	not parallel		
	succ	6	45	0.41	0.523
	unsucc	23	113		
Chase direction		away	not away		
	succ	37	14	0.00	1.000
	unsucc	97	39		
Date				10.67	0.299

key: ** minimum distance <1m or >1m.

Table 2.27. The effect of various recorded parameters on success of chases of all victims by Arctic skuas.

variable		categories				X^2	p
Speed of reaction		Fast	Intermediate	Slow			
	succ	14	17	132		37.66	<0.001
	unsucc	164	135	364			
Attacker's height relative to victim's		Above	Same height	Below			
	succ	123	9	30		3.13	0.210
	unsucc	547	74	156			
Attacker's position relative to victim's		Infront	Side	Behind			
	succ	52	36	28		0.69	0.710
	unsucc	192	125	122			
Victim's initial height		High	Moderate	Low			
	succ	34	6	50		6.57	0.037
	unsucc	124	43	333			
Victim's initial distance from cliff		Far	Moderate	Near			
	succ	11	8	47		16.02	<0.001
	unsucc	126	52	145			
Attacker's initial vertical direction		Descending	Level	Ascending			
	succ	159	21	11		2.89	0.236
	unsucc	710	141	60			
Chase duration		<5secs	5-10secs	10-15secs	>15secs		
	succ	45	89	40	13	15.66	0.001
	unsucc	353	368	146	41		
Average visibility		2-4km	4-10km	10-30km	30-60km		
	succ	10	16	153	76	2.10	0.553
	unsucc	76	72	718	351		
Contact between victim and attacker		contact	no contact				
	succ	94	124			77.72	<0.001
	unsucc	172	888				

continued/

Table 2.27. continued.

variable		categories		X^2	p
		< 1m	> 1m		
Minimum distance	succ	171	38	72.49	<0.001
	unsucc	517	529		
		flapping	no flapping		
Use of flapping by attacker	succ	159	11	3.65	0.056
	unsucc	737	99		
		swoop down	no swoop down		
Use of swoop down by attacker	succ	30	154	0.65	0.420
	unsucc	176	742		
		turn	no turn		
Use of turns by attacker	succ	77	91	21.23	<0.001
	unsucc	231	608		
		towards	not towards		
Chase direction	succ	96	79	10.40	0.001
	unsucc	272	393		
		parallel	not parallel		
Chase direction	succ	62	113	3.35	0.067
	unsucc	186	479		
		away	not away		
Chase direction	succ	63	112	2.20	0.138
	unsucc	283	382		
Date				8.21	0.513

Table 2.28. The effect of various recorded parameters on success of chases of puffins by Arctic skuas.

variable		categories			X^2	p
		Fast	Intermediate	Slow		
Speed of reaction	succ	9	16	110	36.07	<0.001
	unsucc	109	129	269		
		Above	Same height	Below		
Attacker's height relative to victim's	succ	92	7	28	5.15	0.076
	unsucc	351	61	145		
		Infront	Side	Behind		
Attacker's position relative to victim's	succ	46	33	19	0.92	0.631
	unsucc	162	106	83		
		High	Moderate	Low		
Victim's initial height	succ	29	6	43	3.36	0.186
	unsucc	108	35	258		
		Far	Moderate	Near		
Victim's initial distance from cliff	succ	9	6	44	16.80	<0.001
	unsucc	101	46	122		
		Descending	Level	Ascending		
Attacker's initial vertical direction	succ	126	18	11	6.23	0.044
	unsucc	444	119	57		
		<5secs	5-10secs	10-15secs	>15secs	
Chase duration	succ	33	65	38	13	11.00	0.012
	unsucc	208	261	116	30	
		2-4km	4-10km	10-30km	30-60km	
Average visibility	succ	6	10	120	65	4.30	0.231
	unsucc	56	35	469	266	
		contact	no contact			
Contact between victim and attacker	succ	87	93		62.61	<0.001
	unsucc	142	589			

continued/

Table 2.28. continued.

variable		categories		X^2	p
		< 1m	> 1m		
Minimum distance	succ	148	26	56.04	<0.001
	unsucc	390	336		
Use of flapping by attacker		flapping	no flapping		
	succ	142	4	5.21	0.022
	unsucc	543	52		
Use of swoop down by attacker		swoop down	no swoop down		
	succ	17	135	1.31	0.252
	unsucc	97	540		
		turn	no turn		
Use of turns by attacker	succ	70	66	19.75	<0.001
	unsucc	174	391		
		towards	not towards		
Chase direction	succ	80	63	17.69	<0.001
	unsucc	162	292		
		parallel	not parallel		
Chase direction	succ	50	93	0.76	0.383
	unsucc	139	315		
		away	not away		
Chase direction	succ	58	85	1.41	0.234
	unsucc	212	242		
Date				13.42	0.144

Table 2.29. Factors which serve to discriminate between chases by light and melanic Arctic skuas and between chases by Arctic skuas and great skuas. Data are presented for all chases and chases of puffins only.

dependent variable categories	victim	independent variable	change in Rao's V	P
Light and melanic Arctic skuas	All sp	Attacker's initial vertical direction	12.86	<0.001
		Chase duration	6.49	0.011
Light and melanic Arctic skuas	puffin	Attacker's initial vertical direction	8.05	0.005
Arctic skuas and great skuas	All sp	Attacker's initial position	105.98	<0.001
		Minimum distance	33.07	<0.001
		Attacker's initial height	27.13	<0.001
		Use of swoop	20.03	<0.001
		Chase duration	19.18	<0.001
		Use of turns	4.30	0.038
Arctic skuas and great skuas	puffin	Minimum distance	83.23	<0.001
		Use of swoop	46.47	<0.001
		Victim's initial height	31.36	<0.001
		Attacker's initial height	25.75	<0.001
		Use of flapping	18.83	<0.001
		Speed of reaction	22.48	<0.001
		Chase direction,towards	17.01	<0.001
		Chase duration	4.57	0.033

Table 2.30. Differences between light and melanic phase Arctic skuas in terms of chase parameters used in the discriminant analyses. Data for all chases.

variables	categories	attackers: light phase Arctic skuas n[1]	attackers: melanic phase Arctic skuas n[1]	X^2	p
Speed of reaction	Fast	34	141	7.07	0.029
	Intermediate	48	104		
	Slow	114	381		
Attacker's initial position	Infront	65	179	0.77	0.682
	Side	47	116		
	Behind	46	104		
Attacker's initial height	Above	161	496	8.78	0.012
	Same height	29	52		
	Below	62	125		
Victim's initial height	High	47	110	16.88	<0.001
	Moderate	28	22		
	Low	105	276		
Attacker's initial vertical direction	Descending	206	653	12.56	0.002
	Level	58	103		
	Ascending	25	48		
Contact between attacker and victim	Contact	71	200	0.00	1.000
	No contact	258	733		
Minimum distance	< 1m	174	514	0.39	0.530
	> 1m	150	405		
Chase duration	< 5 secs	83	308	15.07	0.002
	5-10 secs	112	338		
	10-15 secs	51	135		
	> 15 secs	25	31		

key:
1. Number of chases within each category for each variable.

Table 2.31. Differences between light and melanic phase Arctic skuas in terms of chase parameters used in the discriminant analyses. Data for chases of puffins only.

		attackers			
variables	categories	light phase Arctic skuas n[1]	melanic phase Arctic skuas n[1]	X^2	p
Speed of reaction	Fast	20	97	8.31	0.016
	Intermediate	47	98		
	Slow	92	288		
Attacker's initial position	Infront	56	153	1.88	0.391
	Side	41	100		
	Behind	35	67		
Attacker's initial height	Above	103	332	9.48	0.009
	Same height	25	43		
	Below	59	116		
Victim's initial height	High	37	100	15.17	<0.001
	Moderate	24	18		
	Low	87	215		
Attacker's initial vertical direction	Descending	128	438	11.71	0.003
	Level	48	89		
	Ascending	24	46		
Contact between attacker and victim	Contact	62	172	0.00	0.951
	No contact	175	498		
Minimum distance	< 1m	145	397	0.36	0.547
	> 1m	88	268		
Chase duration	< 5 secs	45	193	12.86	0.005
	5-10 secs	80	244		
	10-15 secs	44	111		
	> 15 secs	19	26		

key:
1. Number of chases within each category for each variable.

Table 2.32. Differences between Arctic skuas and great skuas in terms of chase parameters used in the discriminant analyses. Data for all chases.

variables	categories	attackers: Arctic skuas n_1	attackers: great skuas n_1	X^2	p
Speed of reaction	Fast	178	173	67.74	<0.001
	Intermediate	154	117		
	Slow	499	167		
Attacker's initial position	Infront	245	21	165.85	<0.001
	Side	164	17		
	Behind	151	152		
Attacker's initial height	Above	673	590	159.47	<0.001
	Same height	83	11		
	Below	189	9		
Victim's initial height	High	160	152	20.56	<0.001
	Moderate	50	20		
	Low	385	203		
Victim's initial distance from cliff	Far	138	57	0.54	0.763
	Moderate	62	25		
	Near	192	90		
Attacker's initial vertical direction	Descending	876	622	106.49	<0.001
	Level	162	14		
	Ascending	73	6		
Contact between attacker and victim	Contact	274	58	55.54	<0.001
	No contact	1013	650		
Minimum distance	< 1m	698	177	157.90	<0.001
	> 1m	567	516		

continued/

Table 2.32. continued.

variables	categories	attackers: Arctic skuas n[1]	attackers: great skuas n[1]	X^2	p
Chase duration	< 5 secs	398	241	27.63	<0.001
	5-10 secs	462	206		
	10-15 secs	187	49		
	> 15 secs	56	15		
Chase direction towards	Towards	370	182	1.54	0.215
	Not towards	476	273		
Chase direction parallel	Parallel	250	83	19.28	<0.001
	Not parallel	596	372		
Chase direction away	Away	348	189	0.01	0.935
	Not away	498	266		
Use of flapping by atacker	Flapping	906	309	214.97	<0.001
	No flapping	110	236		
Use of swoop down by attacker	Swoop down	207	339	241.67	<0.001
	No swoop down	903	276		
Use of turns by attacker	Turns	311	44	121.84	<0.001
	No turns	702	567		
Victim's method of evasion	Dove into water	506	330	10.92	0.001
	Did not dive into water	742	351		

key:
1. Number of chases within each category for each variable.

Table 2.33. Differences between Arctic skuas and great skuas in terms of chase parameters used in the discriminant analyses. Data for chases of puffins only.

variables	categories	attackers: Arctic skuas n_1	attackers: great skuas n_1	X^2	p
Speed of reaction	Fast	118	75	69.87	<0.001
	Intermediate	147	66		
	Slow	382	48		
Attacker's initial position	Infront	209	9	94.67	<0.001
	Side	142	10		
	Behind	102	62		
Attacker's initial height	Above	444	224	73.73	<0.001
	Same height	68	7		
	Below	176	9		
Victim's initial height	High	139	102	33.31	<0.001
	Moderate	42	13		
	Low	303	81		
Victim's initial distance from cliff	Far	111	30	2.06	0.358
	Moderate	54	17		
	Near	166	64		
Attacker's initial vertical direction	Descending	575	238	47.95	<0.001
	Level	137	9		
	Ascending	70	6		
Contact between attacker and victim	Contact	236	13	58.82	<0.001
	No contact	682	275		
Minimum distance	< 1m	546	58	131.47	<0.001
	> 1m	362	222		

continued/

Table 2.33. continued.

variables	categories	attackers: Arctic skuas n[1]	attackers: great skuas n[1]	X^2	p
Chase duration	< 5 secs	241	83	10.49	0.015
	5-10 secs	329	81		
	10-15 secs	155	26		
	> 15 secs	45	8		
Chase direction towards	Towards	243	26	46.21	<0.001
	Not towards	358	167		
Chase direction parallel	Parallel	190	34	13.45	<0.001
	Not parallel	411	159		
Chase direction away	Away	272	136	36.16	<0.001
	Not away	329	57		
Use of flapping by atacker	Flapping	693	146	151.65	<0.001
	No flapping	56	100		
Use of swoop down by attacker	Swoop down	114	116	115.63	<0.001
	No swoop down	681	130		
Use of turns by attacker	Turns	247	16	71.97	<0.001
	No turns	458	228		
Victim's method of evasion	Dove into water	395	137	2.60	0.107
	Did not dive into water	536	148		

key:
1. Number of chases within each category for each variable.

Table 2.34. Speeds of reaction of victims to light and melanic Arctic skuas attacking from different heights. Data for all chases and chases of puffins only.

all species of victim

attacker	speed of reaction	attacker's initial height relative to victims: above n[1]	same height n[1]	below n[1]
Light phase Arctic skuas	Fast	22	4	6
	Intermediate	19	7	17
	Slow	57	8	27
Melanic phase Arctic skuas	Fast	93	8	9
	Intermediate	45	10	33
	Slow	204	18	64

Puffins only

Light phase Arctic skuas	Fast	10	3	6
	Intermediate	18	7	17
	Slow	38	8	26
Melanic phase Arctic skuas	Fast	61	5	9
	Intermediate	42	9	32
	Slow	138	17	58

key:
1. Number of chases within each category.

Table 2.35. Success rates of light and melanic phase Arctic skuas in relation to attacker's initial height relative to that of the victim. Data for all chases and chases of puffins only.

all species of victim

attacker	outcome of chase	attacker's initial relative height: above NO*	above %**	same height NO	same height %	below NO	below %
Light phase Arctic skuas	Victim lost fish	43	26.7	6	20.7	6	9.8
	Victim retained fish	118	73.3	23	79.3	55	90.2
Melanic phase Arctic skuas	Victim lost fish	77	15.6	3	5.8	24	19.5
	Victim retained fish	416	84.4	49	94.2	99	80.5

puffins only

attacker	outcome of chase	attacker's initial relative height: above NO*	above %**	same height NO	same height %	below NO	below %
Light phase Arctic skuas	Victim lost fish	30	29.1	4	16.0	6	10.3
	Victim retained fish	73	70.9	21	84.0	52	89.7
Melanic phase Arctic skuas	Victim lost fish	59	17.8	3	7.0	22	19.3
	Victim retained fish	272	82.2	40	93.0	92	80.7

key:

*. Number of chases within each category.

**. The number of chases within each category expressed as a percentage of the total number of chases initiated from the appropriate height by the appropriate attackers.

Table 2.36. Net energetic reward per unit time chasing of Arctic skuas and great skuas in 1986 and 1987 when chasing various host species.

		Host species		
		puffin	guillemot	razorbill
Arctic skuas 1986	W[1]	54.38kJ	85.00kJ	13.49kJ
	P[2]	0.140	0.092	0.079
	T[3]	8.06+/-0.39s	5.41+/-0.43s	6.64+/-0.71s
	% chases with flapping[4]	92.6	73.1	81.9
	C[5]	0.295kJ	0.160kJ	0.220kJ
	Net E[6]	0.908kJ/s	1.416kJ/s	0.127kJ/s
Arctic skuas 1987	W[1]	54.38kJ	85.00kJ	13.49kJ
	P[2]	0.127	0.100	0.131
	T[3]	7.86+/-0.60s	5.83+/-0.96s	6.09+/-1.01s
	% chases with flapping[4]	92.6	73.1	81.9
	C[5]	0.285kJ	0.180kJ	0.209kJ
	Net E[6]	0.842kJ/s	1.427kJ/s	0.256kJ/s
great skuas 1986	W[1]	82.32kJ	85.00kJ	13.49kJ
	P[2]	0.189	0.120	0.167
	T[3]	6.97+/-0.66s	5.85+/-0.46s	6.48+/-1.99s
	% chases with flapping[4]	59.3	58.5	72.7
	C[5]	0.810kJ	0.670kJ	0.890kJ
	Net E[6]	2.116kJ/s	1.629kJ/s	0.210kJ/s
great skuas 1987	W[1]	82.32kJ	85.00kJ	13.49kJ
	P[2]	0.277	0.135	0.167
	T[3]	9.59+/-2.71s	5.26+/-0.88s	5.61+/-1.78s
	% chases with flapping[4]	59.3	58.5	72.7
	C[5]	1.110kJ	0.610kJ	0.770kJ
	Net E[6]	2.262kJ/s	2.067kJ/s	0.264kJ/s

key:

(1). Calculated from the energy content of an 'average' fish carried by each species of auk in 1987 (Table 3.8) and the average number of fish secured per successful chase of each species of victim by skuas in 1987 (see text chapter 3).

(2). From Table 2.16.

(3). Mean chase duration +/- 2 standard errors.

(4). From data recorded in 1986 only.

(5). Calculated for male skuas on the assumption that flapping during chases costs twice as much as flight at V^{mr} and gliding costs 3.1 times BMR (see chapter 3).

(6). Net energy gain per unit time spent chasing.

Table 3.1. Morphological parameters used in the calculation of basal metabolic rates and the cost of flight.

	Arctic skuas		great skuas	
parameter	male (n=2)	female (n=1)	male (n=11)	female (n=7)
mass(g)	375*	437*	1338+/-62**	1437+/-125**
wingspan(cm)	106.3	109.5	139.9+/-2.1**	143.9+/-2.4**
wing area(cm^2)	1170	1260	2244+/-55**	2481+/-105**
A (m^2)***	1.502E-3	1.652E-3	2.833E-3	2.929E-3
Sd (m^2)****	0.887	0.942	1.538	1.627

key:

*. Masses from Furness (1987a).
**. Mean plus or minus 2 standard errors.
***. Equivalent flat plate area of body. Calculated from mean masses with equations 2,6,7 and 8 of Pennycuick et al.(1988).
****. Wing disc area. Calculated from mean wingspans with equation 6 of Pennycuick (1975).

Table 3.2. Basal and standard metabolic rates, lower critical temperatures and costs of thermoregulation of skuas. Values calculated from the equations of Kendeigh et al. (1977).

	Arctic skuas		great skuas	
parameter	male	female	male	female
SMR at 0°C (kJ/hr)*	18.39	20.06	37.95	39.52
BMR (kJ/hr)**	9.69	10.84	24.64	25.97
Tlc (°C)***	16.14	15.70	12.83	12.66
SMR at T^a (kJ/hr)	12.52	13.66	26.38	27.59
Cost of thermo-regulation at T^a (kJ/hr)	2.83	2.82	1.74	1.62

key:

*. From equation 5.15 of Kendeigh et al.(1977), multipied by 1.367.
**. From equation 5.5 of Kendeigh et al.(1977), multipied by 1.367.
***. From equation 5.12 of Kendeigh et al.(1977). These values are almost certainly over-estimates (see text).

Table 3.3. The absolute minimum power required to fly, the minimum power speed and maximum range speed of skuas. Values calculated from equations of Pennycuick (1975). *

	Arctic skuas		great skuas	
parameter	male	female	male	female
Absolute minimum power needed to fly (P^{am}) (Watts)	1.384	1.699	7.237	7.784
Minimum power speed (V^{mp}) (m/sec)	7.23	7.54	10.16	10.29
Maximum range speed (V^{mr}) (m/sec)	9.51	9.92	13.36	13.54
Cost of flight at V^{mp} (kJ/hr)	66.99	80.45	308.66	331.04
Cost of flight at V^{mp} (multiple of BMR)	6.91	7.42	12.53	12.75
Cost of flight at V^{mr} (kJ/hr)	70.28	84.70	326.03	349.83
Cost of flight at V^{mr} (multiple of BMR)	7.25	7.81	13.23	13.47

*. A value of 1.22g/cm^3 was used for air density. This value corresponds to air density at sea-level (Pennycuick 1969). The value of $\propto$ which was used in the calculations was 7.42 rather than the value of 3.79 given in Pennycuick (1975). The reason for this is that the metabolic rate of South Polar skuas has been found to be 1.96 times the value predicted by the equation of Lasiewski and Dawson (1967), (see text), from which the value of 3.79 was originally derived by Pennycuick (1975).

Table 3.4. Proportion of foraging time spent chasing by Arctic skuas and great skuas. Data recorded in 1987.

	species	
	Arctic skua	great skua
Mean durationion of foraging bouts recorded (seconds)	539 (16)	266 (9)
Proportion of time spent chasing * (%)	10.58 +/- 2.28 (16)	6.45 +/- 2.43 (9)

key:

*. Mean plus or minus 2 standard errors. Values in parentheses are number of observation periods

Table 3.5. Proportion of patrolling periods between chases spent gliding by Arctic skuas. Data recorded in 1986.

Mean duration of patrolling periods observed (seconds)	53 (37)
Proportion of time spent gliding * (%)	47.75 +/- 9.49 (37)

key:

*. Mean plus or minus 2 standard errors. Values in parentheses are number of observation periods.

Table 3.6. Duration of chases by Arctic skuas and great skuas. Chases recorded in 1987 after 15/6.

	species	
	Arctic skua	great skua
Duration of chases* (seconds)	7.25 +/- 0.48 (377)	7.56 +/- 1.28 (94)

key:

*. Mean plus or minus 2 standard errors. Values in parentheses are number of chases recorded.

Table 3.7. Host selection patterns and success rates in securing fish of Arctic skuas and great skuas in 1987 (after 15/6).

		attacker	
	victim	Arctic skua	great skua
Total number of chases recorded	All	500	211
Number of chases of each species of victim *	puffin	385 (77.0%)	93 (44.1%)
	guillemot	67 (13.4%)	86 (40.8%)
	razorbill	48 (9.6%)	10 (4.7%)
	gannet	0 -	22 (10.4%)
Number of chases in which attacker secured fish **	puffin	47 (12.2%)	26 (28.0%)
	guillemot	3 (4.5%)	12 (14.0%)
	razorbill	7 (14.6%)	2 (20.0%)
	gannet	0 -	3 (13.6%)

key:

*. Values in parentheses are the proportions of the total number of chases recorded which were of each host species.

**. Values in parentheses are the proportions of the total number of chases of each host species in which the attackers secured fish.

Table 3.8. Percentages of numbers, lengths, weights, calorific values and energy contents of fish carried by the main host species of skuas in 1987.

parameter	host species	species of fish: sandeel	sprat	other (haddock)
proportion of fish sample *	puffin	66.7% (6)	0%	33.3% (3)
	guillemot	54.2% (13)	45.8% (11)	0%
	razorbill	100.0% (7)	0%	0%
mean fish length +/- 2se (cm)	puffin	13.77+/-1.25	-	7.68+/-2.11
	guillemot	15.13+/-1.18	10.56+/-0.29	-
	razorbill	8.81+/-1.48	-	-
mean fish weight (g) **	puffin	8.04	-	3.84
	guillemot	10.82	8.12	-
	razorbill	1.97	-	-
mean calorific value (kJ/g)***	puffin	7.937	-	5.73(a)
	guillemot	8.237	9.868	-
	razorbill	6.846	-	-
mean energy content of one fish (kJ)	puffin	63.82	-	22.00
	guillemot	89.12	80.13	-
	razorbill	13.49	-	-

mean energy content of an 'average' fish carried by the main host species. (b)

puffin	guillemot	razorbill	gannet(c)
49.89kJ	85.00kJ	13.49kJ	89.12kJ

key:

*. Numbers in parentheses are sample sizes.
**. Calculated from equations in appendix of Harris and Hislop (1978).
***. Calculated from equations in Harris and Hislop (1978).
(a). Calculated from data in Table II of Harris and Hislop (1978).
(b). Allowing for the proportions of differeent fish types carried.
(c). Assumes that gannets carried only sandeels of the same size as guillemots.

Table 3.9. Number of foraging trips, time spent travelling to and from cliffs, hours absent from territory and hours per day spent actually foraging by great skuas and Arctic skuas.

species/ pair/sex	parameter: mean number of foraging trips per day	mean number of minutes spent commuting per day *	mean number of hours absent per day	hours foraging per day **
great skua				
pair A				
male	3.80	18.96	13.52 +/- 2.85	13.21
female	4.33	21.30	13.22 +/- 2.99	12.87
pair B				
male	4.50	22.46	11.58 +/- 2.62	11.20
female	3.87	19.04	10.95 +/- 2.60	10.63
pair D/E				
male	5.13	25.60	14.17 +/- 3.02	13.74
female	3.83	18.84	11.05 +/- 2.62	10.74
Arctic skua				
pair X				
male	8.33	29.16	9.37 +/- 2.64	8.89
female	6.83	22.95	6.88 +/- 2.55	6.50
pair Y				
male	9.50	33.25	6.28 +/- 1.91	5.73
female	7.00	23.52	4.96 +/- 2.20	4.56
pair Z				
male	10.33	36.16	8.36 +/- 2.50	7.76
female	5.00	16.80	7.35 +/- 2.59	7.07

key:

*. Assuming commuting distances of 4km per trip for great skuas and 2km per trip for Arctic skuas are covered at V^{mr} (the speed at which distance covered over the ground per unit energy expended is maximal).

**. Calculated by subtracting mean time spent travelling to and from cliffs per day from the mean number of hours absent from the territory per day.

Table 3.10. Percentage of time spent in various activities during the chick-rearing period, and energy expended in these activities by male and female great skuas (Pair A).

	male		female	
activity	% of time spent in each activity	energy expended (kJ/hr)	% of time spent in each activity	energy expended (kJ/hr)
Absent (foraging)*	56.35%	120.37	55.10%	126.19
Resting	39.30%	14.53	39.43%	15.36
Other**	4.34%	3.43	5.46%	3.80
Thermoregulation	-	0.75	-	0.72
Total energy expended per hour		139.08kJ		146.07kJ
Total energy expended per day		3,338kJ		3,506kJ
Energy requirements of chicks per day		3,531kJ		
Total daily requirements		10,375kJ/day		
Total assimilated input		12,498kJ/day (8,640kJ/day)***		

key:

*. Includes periods of flying to and from cliff faces.
**. Includes activity in all other categories.
***. Assimilated input calculated with energy content of modal length fish collected from auks on Foula between 1971 and 1980 (Furness unpbl.).

Table 3.11. Percentage of time spent in various activities during the chick-rearing period, and energy expended in these activities by male and female great skuas (Pair B).

	male		female	
activity	% of time spent in each activity	energy expended (kJ/hr)	% of time spent in each activity	energy expended (kJ/hr)
Absent * (foraging)	48.23%	103.53	45.63%	104.62
Resting	47.00%	17.37	46.58%	18.15
Other**	4.78%	2.95	7.80%	4.93
Thermoregulation	-	0.90	-	0.88
Total energy expended per hour		124.75kJ		128.58kJ
Total energy expended per day		2,994kJ		3,086kJ
Energy requirements of chick per day		1,736kJ		
Total daily requirements		7,816kJ/day		
Total assimilated input		10,465kJ/day (7,234kJ/day)***		

key:

*. Includes periods of flying to and from cliff faces.
**. Includes activity in all other categories.
***. Assimilated input calculated with energy content of modal length fish collected from auks on Foula between 1971 and 1980 (Furness unpbl.).

Table 3.12. Percentage of time spent in various activities during the chick-rearing period, and energy expended in these activities by male and female great skuas (Pairs D/E).

	male		female	
activity	% of time spent in each activity	energy expended (kJ/hr)	% of time spent in each activity	energy expended (kJ/hr)
Absent * (foraging)	59.04%	126.57	46.06%	105.57
Resting	35.13%	12.98	49.68%	19.35
Other**	5.84%	3.62	4.26%	3.08
Thermoregulation	-	0.71	-	0.87
Total energy expended per hour		143.88kJ		128.87kJ
Total energy expended per day		3,453kJ		3,093kJ
Energy requirements of chicks per day		3,555kJ		
Total daily requirements		10,101kJ/day		
Total assimilated input		11,733kJ/day (8,112kJ/day)***		

key:

*. Includes periods of flying to and from cliff faces.
**. Includes activity in all other categories.
***. Assimilated input calculated with energy content of modal length fish collected from auks on Foula between 1971 and 1980 (Furness unpbl.).

Table 3.13 Percentage of time spent in various activities during the chick-rearing period, and energy expended in these activities by male and female Arctic skuas (Pair X).

	male		female	
activity	% of time spent in each activity	energy expended (kJ/hr)	% of time spent in each activity	energy expended (kJ/hr)
Absent (foraging)*	39.06%	22.82	28.68%	19.85
Resting	46.09%	6.70	58.18%	9.46
Other**	14.83%	6.93	13.11%	8.12
Thermoregulation	-	1.62	-	1.90
Total energy expended per hour		38.07kJ		39.33kJ
Total energy expended per day		914kJ		944kJ
Energy requirements of chicks per day		2,358kJ		
Total daily requirements		4,216kJ/day		
Total assimilated input		3,762kJ/day (1,781kJ/day)***		

key:

*. Includes periods of flying to and from cliff faces.
**. Includes activity in all other categories.
***. Assimilated input calculated with energy content of modal length fish collected from auks on Foula between 1971 and 1980 (Furness unpbl.).

Table 3.14. Percentage of time spent in various activities during the chick-rearing period, and energy expended in these activities by male and female Arctic skuas (Pair Y).

	male		female	
activity	% of time spent in each activity	energy expended (kJ/hr)	% of time spent in each activity	energy expended (kJ/hr)
Absent (foraging)*	26.18%	15.41	20.65%	14.37
Resting	57.80%	8.40	64.02%	10.41
Other**	16.02%	7.17	15.32%	8.68
Thermoregulation	-	1.99	-	2.13
Total energy expended per hour		32.97kJ		35.59kJ
Total energy expended per day		791kJ		854kJ
Energy requirements of chick per day		555kJ		
Total daily requirements		2,200kJ/day		
Total assimilated input		2,516kJ/day (1,191kJ/day)***		

key:

*. Includes periods of flying to and from cliff faces.
**. Includes activity in all other categories.
***. Assimilated input calculated with energy content of modal length fish collected from auks on Foula between 1971 and 1980 (Furness unpbl.).

Table 3.15. Percentage of time spent in various activities during the chick-rearing period, and energy expended in these activities by male and female Arctic skuas (Pair Z).

	male		female	
activity	% of time spent in each activity	energy expended (kJ/hr)	% of time spent in each activity	energy expended (kJ/hr)
Absent * (foraging)	34.84%	20.43	30.63%	21.11
Resting	53.33%	7.75	55.18%	8.97
Other**	11.82%	6.51	14.18%	8.73
Thermoregulation	-	1.75	-	1.85
Total energy expended per hour		36.44kJ		40.66kJ
Total energy expended per day		875kJ		976kJ
Energy requirements of chicks per day		1,490kJ		
Total daily requirements		3,341kJ/day		
Total assimilated input		3,626kJ/day (1,717kJ/day)***		

key:

*. Includes periods of flying to and from cliff faces.
**. Includes activity in all other categories.
***. Assimilated input calculated with energy content of modal length fish collected from auks on Foula between 1971 and 1980 (Furness unpbl.).

Table 3.16. DEEs of Arctic skuas and great skuas as determined in this study and a compilation of DEEs of birds from other studies.

species	period of yearly cycle	DEE (kJ/day)	DEE (xBMR)	reference
Arctic skua (female)	chick rearing	944	3.63(1)	This study
"	"	854	3.28(1)	"
"	"	976	3.75(1)	"
Arctic skua (male)	"	914	3.93(1)	"
"	"	791	3.40(1)	"
"	"	875	3.76(1)	"
great skua (female)	"	3506	5.62(1)	"
"	"	3086	4.95(1)	"
"	"	3093	4.96(1)	"
great skua (male)	"	3338	5.64(1)	"
"	"	2994	5.06(1)	"
"	"	3453	5.84(1)	"
Arctic skua (male)	small chicks	617	2.53(1)	Furness 1980
"	medium chicks	600	2.46(1)	"
"	large chick	599	2.46(1)	"

continued/

Table 3.16. continued.

species	period of yearly cycle	DEE (kJ/day)	DEE (xBMR)	reference
Arctic skua (female)	small chicks	554	2.27(1)	Furness 1980
"	medium chicks	554	2.27(1)	"
"	large chick	559	2.29(1)	"
Arctic skua	post breeding	403	2.14(3)	Birt and Cairns 1987
"	"	452	2.40(3)	"
lesser sheathbill (male)	chick rearing	657	3.09(3)	Burger 1981
lesser sheathbill (female)	"	613	3.15(3)	"
king penguin	chick rearing	6852	3.27(3)	Kooyman et al.1982
gentoo penguin	chick rearing	3803	3.1(3)	Davis et al.1983 cited from Ellis 1984
macaroni penguin	"	2830	3.4(3)	"
wedge-tailed shearwater	incubation	614	4.8(4)	Ellis 1984
brown noddy	incubation	352	5.2(4)	"

continued/

Table 3.16. continued.

species	period of yearly cycle	DEE (kJ/day)	DEE (xBMR)	reference
sooty tern	incubation (on nest)	141	1.62(4)	Flint and Nagy 1984
"	incubation (off nest)	340	4.00(4)	"
jackass penguin	chick rearing	1945	2.58(3)	Nagy et al.1984
thick-billed murre	chick rearing	1527	4.72(2)	Gaston 1985
"	"	1393	4.18(2)	"
black guillemot	"	943	5.28(2)	"
wandering albatross	chick rearing	3354	1.83(4)	Adams et al.1986
little penguin	pre-laying (foraging)	982	2.15(5)	Costa et al.1986
"	pre-laying (onshore)	619	1.31(5)	"
leach's storm petrel	chick rearing (at sea)	123	2.82(4)	Ricklefs et al. 1986
"	incubation	52	1.19(4)	"

continued/

Table 3.16. continued.

species	period of yearly cycle	DEE (kJ/day)	DEE (xBMR)	reference
least auklet	chick rearing	358	3.08(5)	Roby and Ricklefs 1986
South Georgia diving petrel	"	464	4.15(5)	"
common diving petrel	"	557	4.27(5)	"
grey-headed albatross	incubation (at sea)	2393	2.47(6)	Costa and Prince 1987
"	incubation (at sea and onshore)	1728	1.76(6)	"
Wilson's storm petrel	incubation (on nest)	81	2.19(4)	Obst et al.1987
"	incubation (at sea)	157	4.21(4)	"
"	incubation /brooding (on nest and at sea)	119	3.19(4)	"
"	chick rearing (on nest and at sea)	157	4.21(4)	"
laysan albatross (male)	incubation (at sea and onshore)	1169	1.54(4)	Pettit et al.1988

continued/

Table 3.16. continued.

species	period of yearly cycle	DEE (kJ/day)	DEE (xBMR)	reference
laysan albatross (female)	"	1457	2.13(4)	Pettit et al.1988
purple martin (female)	chick rearing	167-184	2.8-3.1(3)	Utter and LeFebvre 1973
purple martin (male)	"	130-143	2.1-2.3(3)	"
black-shouldered kite	non breeding	411	3.21(6)	Tarboton 1978
house martin	chick rearing	58-137	2.22-5.27(5)	Hails and Bryant 1979
Pacific swallow	chick rearing	77	5.1(4)	Bryant et al.1984
blue-throated bee-eater	"	77	3.0(4)	"
Abert's towhee (female)	chick rearing	109	1.80(4)	Finch 1984
Abert's towhee (male)	chick rearing	115	1.93(4)	"
European starling (female)	chick rearing	331	4.00(3)-4.52(6)	Ricklefs and Williams 1984
European starling (male)	"	272	3.23(3)-3.65(6)	"

continued/

Table 3.16. continued.

species	period of yearly cycle	DEE (kJ/day)	DEE (xBMR)	reference
house martin (female)	incubation	-	2.7(6)	Bryant and Westerterp 1980 cited from Ricklefs and Williams 1984
house martin (both sexes)	chick rearing	-	3.59(6)	"
loggerhead shrike	non breeding	106	2.47(4)	Weathers et al.1984
house martin (male)	chick rearing	81	3.00(6)	Westerterp and Bryant 1984
"	"	102	3.77(6)	"
house martin (female)	"	76	2.87(6)	"
"	"	103	3.86(6)	"
sand martin (male)	"	94	4.42(6)	"
sand martin (female)	"	90	4.21(6)	"
swallow (male)	"	111	3.98(6)	"
swallow (female)	"	109	3.84(6)	"
savannah sparrow	pre-lay incubation	80	2.84(7)	Williams and Nagy 1984
phainopepla	?	84	2.63(7)	"

continued/

Table 3.16. continued.

species	period of yearly cycle	DEE (kJ/day)	DEE (xBMR)	reference
budgerygah	summer non-breeding	83	2.74(4)	Buttemer et al. 1986
"	winter non-breeding	97	2.94(4)	"
European kestrel (male)	chick rearing	396	4.14(4)	Masman et al.1988
European kestrel (female)	"	345	3.38(4)	"

key:

(1). BMR = 1.367 times BMR from Kendeigh et al.1977 (Eqn 5.5).
(2). BMR from Kendeigh et al.1977 (Eqn 5.5).
(3). BMR from Lasiewski and Dawson 1967.
(4). BMR measured.
(5). SMR measured.
(6). BMR from Aschoff and Pohl 1970.
(7). BMR from Kendeigh et al.1977 (Eqn 5.1).

Table 4.1. Comparisons of the mean territorial attendance values of early and late-laying pairs of skuas. 1987 data only.

species	brood size	<MLD*	>MLD*	statistic	P**
Pre-laying period					
Arctic skua	1	1.398 (8,276)	1.611 (2,99)	U=0.0	0.044
Arctic skua	2	1.324 (7,302)	1.539 (4,101)	U=10.0	0.527
great skua	1	1.500 (6,268)	1.358 (4,234)	U=5.0	0.172
great skua	2	1.393 (12,523)	1.408 (5,271)	U=29.0	0.959
Incubation period					
Arctic skua	1	1.766 (8,341)	1,803 (2,76)	U=5.0	0.533
Arctic skua	2	1.768 (7,297)	1.759 (4,150)	U=10.0	0.527
great skua	1	1.508 (5,268)	1.571 (4,181)	U=8.0	0.730
great skua	2	1.559 (12,632)	1.532 (4,183)	U=14.5	0.262
Early pre-fledging period					
Arctic skua	1	1.817 (8,97)	1.778 (2,13)	U=7.0	0.889
Arctic skua	2	1.776 (6,69)	1.600 (4,26)	U=2.5	0.038
great skua	1	1.578 (5,74)	1.487 (3,47)	U=5.0	0.571
great skua	2	1.612 (12,199)	1.324 (4,73)	U=7.0	0.042
Late pre-fledging period					
Arctic skua	1	1.621 (6,127)	1.275 (2,48)	U=0.0	0.071
Arctic skua	2	1.561 (5,102)	1.380 (4,64)	U=6.0	0.413
great skua	1	1.214 (4,181)	1.051 (1,39)	U=2.0	1.000
great skua	2	0.996 (6,267)	0.806 (1,31)	U=0.0	0.286
post-fledging period					
Arctic skua	1	1.515 (6,70)	-	-	-
Arctic skua	2	1.286 (4,35)	-	-	-
great skua	1	1.132 (2,51)	-	-	-
great skua	2	0.535 (3,97)	0.650 (1,20)	U=1.0	1.000

key:

*. Values given are the averages of the mean territorial attendance values of the pairs of skuas within the appropriate category. Values in parentheses are firstly the number of pairs within each category and secondly the total number of spot observations made on all the pairs within that category during the appropriate period of the breeding season.

**. All probabilities given are two-tailed.

*. <MLD = pairs which laid on or before the Mean Laying Date
>MLD = pairs which laid after the Mean Laying Date

Table 4.2. Comparison within and between periods of the mean territorial attendance values of pairs of Arctic skuas. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	1.398 (8)	1.324 (7)	U=20.5	0.397
	U=0.0 p<0.001	U=0.0 p<0.001		
Incubation	1.766 (8) *	1.768 (7) *	U=26.0	0.867
	U=31.5 p=0.480	U=16.0 p=0.267		
Early pre-fledge	1.817 (8) *	1.776 (6) *	U=20.5	0.331 *
	U=7.0 p=0.015	U=4.0 p=0.026		
Late pre-fledge	1.621 (6) *	1.561 (5) *	U=14.0	0.465 *
	U=9.5 p=0.090	U=1.0 p=0.016		
Post-fledge	1.515 (6)	1.288 (4)	U=2.0	0.019 *
Late-laying pairs				
Pre-laying	1.611 (2)	1.539 (4)	U=4.0	1.000
	U=0.0 p=0.333	U=2.0 p=0.114		
Incubation	1.803 (2) *	1.759 (4) *	U=4.0	1.000
	U=2.0 p=0.500	U=3.0 p=0.100		
Early pre-fledge	1.778 (2) *	1.600 (4) *	U=3.0	0.400 *
	U=0.0 p=0.167	U=3.0 p=0.100		
Late pre-fledge	1.275 (2)	1.380 (4)	U=3.0	0.400 *

key:

a. Values given are the averages of the mean territorial attendance scores of the pairs of skuas within the appropriate category. Values in parentheses are the number of pairs within each category.

b. Probabilities marked with an asterisk (*) are one tailed. All other probabilities given are two tailed.

Table 4.3. Comparison within and between periods of the mean territorial attendance values of pairs of great skuas. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	1.500 (6)	1.393 (12)	U=21.5	0.180
	U=15.0 p=1.000	U=17.5 p<0.001		
Incubation	1.508 (5) *	1.559 (12) *	U=19.5	0.279
	U=9.0 p=0.274	U=49.0 p=0.099		
Early pre-fledge	1.573 (5) *	1.612 (12) *	U=27.5	0.400 *
	U=3.0 p=0.056	U=0.0 p<0.001		
Late pre-fledge	1.214 (4) *	0.996 (6) *	U=4.0	0.057 *
	U=4.0 p=0.500	U=0.0 p=0.012		
Post-fledge	1.132 (2)	0.535 (3)	U=2.0	0.400 *
Late-laying pairs				
Pre-laying	1.358 (4)	1.408 (5)	U=7.0	0.556
	U=1.0 p=0.057	U=6.0 p=0.413		
Incubation	1.571 (4) *	1.532 (4) *	U=6.0	0.686
	U=2.0 p=0.114	U=3.0 p=0.100		
Early pre-fledge	1.487 (3) *	1.324 (4) *	U=4.0	0.314 *
	U=0.0 p=0.250	U=0.0 p=0.200		
Late pre-fledge	1.051 (1)	0.806 (1) *	U=0.0	0.500 *
	- -	U=0.0 p=0.500		
Post-fledge	-	0.650 (1)	-	-

key:
as for Table 4.2.

Table 4.4. Comparison within and between periods of the percentage of adult Arctic skuas seen on their territories during spot observations. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	70.1 (26) z=-3.80 p<0.001	66.6 (26) z=-3.97 p<0.001	z=-0.71	0.475
Incubation	88.3 (25) * z=-0.98 p=0.163	87.6 (26) * z=-0.54 p=0.294	z=-0.61	0.545
Early pre-fledge	91.2 (6) * U=23.0 p=0.047	86.3 (5) * U=15.0 p=0.047	U=9.0	0.165*
Late pre-fledge	83.6 (15) * U=34.0 p=0.024	78.1 (13) * U=2.5 p<0.001	U=62.0	0.054*
Post-fledge	71.2 (9)	57.0 (7)	U=14.5	0.036*
Late-laying pairs				
Pre-laying	78.5 (37) z=-1.05 p=0.293	80.8 (24) z=-0.75 p=0.456	z=-0.19	0.849
Incubation	88.2 (23) * z=-1.04 p=0.150	86.7 (26) * z=-1.59 p=0.056	z=-0.93	0.354
Early pre-fledge	75.0 (5) * U=39.0 p=0.290	76.7 (5) * U=32.0 p=0.162	U=11.5	0.421*
Late pre-fledge	67.3 (19)	68.3 (18)	U=164.0	0.423*

key:

a. Values given are the averages, over the appropriate period, of the percentage of adult skuas seen on their territories during each day of that period. Values in parentheses are the number of days of observation during each period of the breeding season on which sufficient observations were made for the percentage of adults present on their territories to be calculated.

b. Probabilities marked with an asterisk (*) are one tailed. All other probabilities given are two tailed. z values corrected for ties are presented where the larger of the two independent groups exceeds 20 in size (see Siegel 1956).

Table 4.5. Comparison within and between periods of the percentage of adult great skuas seen on their territories during spot observations. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	76.6 (21)	69.2 (21)	z=-1.95	0.051
	z=-0.67 p=0.501	z=-2.98 p=0.003		
Incubation	73.8 (30) *	77.9 (30) *	z=-1.53	0.125
	z=-1.08 p=0.139	z=-1.35 p=0.088		
Early pre-fledge	78.6 (8) *	82.7 (9) *	U=26.0	0.185*
	z=-3.76 p<0.001	z=-4.28 p<0.001		
Late pre-fledge	58.0 (29) *	51.1 (29) *	z=-1.68	0.046*
	z=-0.63 p=0.265	z=-4.99 p<0.001		
Post-fledge	55.7 (21)	23.8 (22)	z=-4.96	<0.001*
Late-laying pairs				
Pre-laying	66.7 (35)	71.1 (35)	z=-0.84	0.399
	z=-2.39 p=0.017	z=-1.21 p=0.228		
Incubation	77.9 (26) *	75.6 (24) *	z=-0.90	0.369
	z=-1.75 p=0.040	z=-3.32 p<0.001		
Early pre-fledge	72.0 (14) *	63.2 (14) *	U=45.0	0.007*
	z=-4.48 p<0.001	U=31.0 p<0.001		
Late pre-fledge	44.4 (26) *	33.7 (20) *	z=-2.06	0.020*
	z=-0.22 p=0.412	U=22.5 p=0.257		
Post-fledge	41.7 (3)	33.3 (3)	U=4.0	0.500*

key:

as for Table 4.4.

Table 4.6. Comparison within and between periods of the percentage of occasions on which both adults of a pair of Arctic skuas were seen together on their territory. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	63.8 (26)	57.5 (26)	z=-1.12	0.264
	z=-2.49 p=0.013	z=-3.04 p=0.002		
Incubation	76.9 (25) *	75.4 (26) *	z=-0.62	0.533
	z=-0.96 p=0.170	z=-0.57 p=0.285		
Early pre-fledge	80.1 (6) *	72.6 (5) *	U=9.0	0.165*
	U=23.0 p=0.047	U=15.0 p=0.047		
Late pre-fledge	67.1 (15) *	59.9 (13) *	U=63.0	0.059*
	U=34.0 p=0.024	U=1.5 p<0.001		
Post-fledge	44.7 (9)	18.9 (7)	U=14.5	0.036*
Late-laying pairs				
Pre-laying	70.5 (37)	74.2 (24)	z=-0.02	0.988
	z=-0.65 p=0.517	z=-0.04 p=0.969		
Incubation	77.5 (23) *	74.3 (26) *	z=-0.97	0.332
	z=-1.07 p=0.143	z=-1.68 p=0.047		
Early pre-fledge	50.0 (5) *	53.3 (5) *	U=11.5	0.421*
	U=39.0 p=0.290	U=32.0 p=0.182		
Late pre-fledge	34.7 (19)	36.6 (18)	U=164.0	0.423*

key:
a. Values given are the averages, over the appropriate period, of the percentage of occasions on which both adults of a pair were seen together on their territory on each day of that period. Values in parentheses are the number of days of observation during each period of the breeding season on which sufficient observations were made for the aforementioned parameter to be calculated.
b. Probabilities marked with an asterisk (*) are one tailed. All other probabilities given are two tailed. z values corrected for ties are presented where the larger of the two independent groups exceeds 20 in size (see Siegel 1956).

Table 4.7. Comparison within and between periods of the percentage of occasions on which both adults of a pair of great skuas were seen together on their territory. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	60.3 (21)	48.3 (21)	z=-1.73	0.084
	z=-1.73 p=0.084	z=-1.78 p=0.075		
Incubation	47.6 (30) *	56.0 (30) *	z=-1.56	0.120
	z=-1.08 p=0.139	z=-1.35 p=0.088		
Early pre-fledge	57.1 (8) *	65.4 (9) *	U=26.0	0.185*
	z=-3.65 p<0.001	z=-4.26 p<0.001		
Late pre-fledge	22.1 (29) *	16.8 (29) *	z=-1.49	0.068*
	z=-2.74 p=0.003	z=-2.94 p=0.002		
Post-fledge	35.6 (21)	5.4 (22)	z=-4.95	<0.001*
Late-laying pairs				
Pre-laying	45.0 (35)	52.0 (35)	z=-1.09	0.276
	z=-1.64 p=0.101	z=-0.27 p=0.789		
Incubation	55.7 (26) *	51.1 (24) *	z=-0.90	0.369
	z=-1.72 p=0.042	z=-3.31 p<0.001		
Early pre-fledge	44.1 (14) *	26.4 (14) *	U=45.0	0.007*
	z=-4.42 p<0.001	U=51.0 p<0.001		
Late pre-fledge	8.3 (26) *	9.6 (20) *	z=-0.45	0.328*
	z=-0.46 p=0.325	U=24.5 p=0.317		
Post-fledge	16.7 (3)	33.3 (3)	U=4.0	0.500*

key:

as for Table 4.6.

Table 4.8. Comparison within and between periods of the percentage of occasions on which both adults of a pair of Arctic skuas were absent from their territory at the same time. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	23.7 (26) z=-5.21 p<0.001	24.3 (26) z=-5.29 p<0.001	z=-0.21	0.832
Incubation	0.3 (25) z=-0.49 p=0.312 *	0.3 (26) z=-0.44 p=0.331 *	z=0.00	1.000
Early pre-fledge	0.0 (6) U=45.0 p=0.500 *	0.0 (5) U=30.0 p=0.425 *	U=15.0	0.500 *
Late pre-fledge	0.0 (15) U=60.0 p=0.341 *	0.6 (13) U=28.0 p=0.091 *	U=90.0	0.376 *
Post-fledge	2.2 (9)	5.0 (7)	U=23.0	0.204 *
Late-laying pairs				
Pre-laying	13.5 (37) z=-2.45 p=0.014	12.5 (24) z=-3.17 p=0.002	z=-0.38	0.707
Incubation	1.1 (23) z=-0.47 p=0.321 *	1.0 (26) z=-0.44 p=0.331 *	z=-0.09	0.930
Early pre-fledge	0.0 (5) U=47.5 p=0.500 *	0.0 (5) U=45.0 p=0.500 *	U=12.5	0.500 *
Late pre-fledge	0.0 (19)	0.0 (18)	U=171.0	0.500 *

key:

a. Values given are the averages, over the appropriate period, of the percentage of occasions on which both adults of a pair were absent from their territory at the same time on each day of that period. Values in parentheses are the number of days of observation during each period of the breeding season on which sufficient observations were made for the aforementioned parameter to be calculated.

b. Probabilities marked with an asterisk (*) are one tailed. All other probabilities given are two tailed. z values corrected for ties are presented where the larger of the two independent groups exceeds 20 in size (see Siegel 1956).

Table 4.9. Comparison within and between periods of the percentage of occasions on which both adults of a pair of great skuas were absent from their territory at the same time. 1987 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Early-laying pairs				
Pre-laying	7.2 (21) z=-4.40 p<0.001	9.9 (21) z=-5.12 p<0.001	z=-1.06	0.288
Incubation	0.0 (30) * z=0.00 p=0.500	0.2 (30) * z=-0.55 p=0.292	z=-1.00	0.317
Early pre-fledge	0.0 (8) * z=-1.51 p=0.065	0.0 (9) * z=-2.63 p=0.004	U=36.0	0.500 *
Late pre-fledge	6.2 (29) * z=-3.46 p<0.001	14.5 (29) * z=-5.25 p<0.001	z=-2.15	0.016 *
Post-fledge	24.2 (21)	58.2 (22)	z=-4.09	<0.001 *
Late-laying pairs				
Pre-laying	11.6 (35) z=-3.60 p<0.001	9.8 (35) z=-3.63 p<0.001	z=-0.09	0.932
Incubation	0.0 (26) * z=0.00 p=0.500	0.0 (24) * z=0.00 p=0.500	z=0.00	1.000
Early pre-fledge	0.0 (14) * z=-3.43 p<0.001	0.0 (14) * U=35.0 p<0.001	U=98.0	0.500 *
Late pre-fledge	19.6 (26) * z=-0.15 p=0.440	42.2 (20) * U=20.5 p=0.202	z=-2.27	0.012 *
Post-fledge	33.3 (3)	66.7 (3)	U=3.0	0.350 *

key:

as for Table 4.8.

Table 4.10. Comparison within and between periods of the mean territorial attendance values of pairs of great skuas. 1986 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Incubation	1.505 (2,32)* U=1.0 p=0.333	1.778 (1,9) * U=0.0 p=0.333	U=0.0	0.667
Early pre-fledge	1.307 (2,47)* U=1.0 p=0.133	1.300 (2,36)* U=1.0 p=0.133	U=2.0	0.500*
Late pre-fledge	1.121 (4,133)	1.057 (4,157)	U=6.0	0.343*

key:

a. Values given are the averages of the mean territorial attendance scores of the pairs of skuas within the appropriate category. Values in parentheses are firstly the number of pairs within each category and secondly the total number of spot observations made on all the pairs within thst category during the appropriate period of the breeding season.
b. Probabilities marked with an asterisk (*) are one tailed. All other probabilities given are two tailed.

Table 4.11. Comparison within and between periods of the mean territorial attendance values of pairs of Arctic skuas. 1986 data only.

period	brood size 1[a]	brood size 2[a]	statistic	P[b]
Incubation	1.613 (2,48)*	1.470 (3,23)*	U=2.0	0.800
	U=1.0 p=0.333	U=5.0 p=0.429		
Early pre-fledge	1.509 (2,30)*	1.479 (4,31)*	U=3.0	0.400*
	U=0.0 p=0.333	U=8.0 p=0.365		
Late pre-fledge	1.000 (1,34)	1.380 (5,127)*	U=0.0	0.167*
	- -	U=4.0 p=0.095		
Post-fledge	-	1.210 (4,81)	-	-

key:

as for Table 4.10.

Table 4.12. Comparison of the mean territorial attendance values of great skuas studied in 1986 and 1987.

period	brood size	1986[a]	1987[a]	statistic	P[b]
Incubation	1	1.505 (2)	1.536 (9)	U=8.0	0.909
	2	1.778 (1)	1.552 (16)	U=0.0	0.118
Early pre-fledge	1	1.307 (2)	1.544 (8)	U=1.0	0.089
	2	1.300 (2)	1.540 (16)	U=6.0	0.209
Late pre-fledge	1	1.121 (4)	1.181 (5)	U=10.0	1.000
	2	1.057 (4)	0.968 (7)	U=7.0	0.230

key:

as for Table 4.2.

Table 4.13. Comparison of the mean territorial attendance values of Arctic skuas studied in 1986 and 1987.

period	brood size	1986[a]	1987[a]	statistic	P[b]
Incubation	1	1.613 (2)	1.774 (10)	U=5.0	0.364
	2	1.470 (3)	1.764 (11)	U=7.5	0.170
Early pre-fledge	1	1.509 (2)	1.809 (10)	U=1.0	0.061
	2	1.479 (4)	1.705 (10)	U=9.0	0.142
Late pre-fledge	1	1.000 (1)	1.534 (8)	U=0.0	0.222
	2	1.380 (5)	1.480 (9)	U=14.5	0.298
Post-fledge	2	1.210 (4)	1.288 (4)	U=7.0	0.886

key:

as for Table 4.2.

Table 4.14. Comparison of the mean territorial attendance values, during the later part of the pre-fledging period, of great skuas studied in 1976 and in 1986 and 1987.

period	brood size	1976[a]	1986-87[a]	statistic	P[b]
Late pre-fledge	1	1.567 (2)	1.154 (9)	U=2.0	0.146
	2	1.367 (2)	1.001 (11)	U=0.0	0.026
	1&2	1.467 (4)	1.070 (20)	U=5.0	0.003

key:

as for Table 4.2.

Table 4.15. Comparison of the territorial attendance patterns of Arctic skuas with a clutch/brood of one(*) recorded in 1979 with those recorded in 1986 and 1987.

period	N° of adults present	year: 1979	year: 1986 & 1987	X^2	P
Incubation	1	11	42	0.03	0.80<P<0.90
	2	21	81		
Early pre-fledge	1	6	37	0.25	0.50<P<0.70
	2	24	103		
Late pre-fledge	1	7	116	12.70	<0.001
	2	31	111		

key:

*. Pairs studied in 1979 had clutches and hence broods of one. Of those pairs studied in 1986 and 1987 only two out of twelve pairs used in the analysis of attendance during the pre-fledging period actually layed only one egg. The other pairs layed two eggs of which only one hatched or one of the chicks was assumed to have died young.

Table 4.16. Comparison of the territorial attendance patterns of Arctic skuas with a clutch/brood of two recorded in 1979 with those recorded in 1986 and 1987.

period	N° of adults present	year		X^2	P
		1979	1986 & 1987		
Incubation	1	50	265	1.36	0.20<P<0.30
	2	191	815		
Early pre-fledge	1	10	43	3.47	0.05<P<0.10
	2	43	83		
Late pre-fledge	1	24	180	8.12	0.001<P<0.01
	2	38	123		

Table 4.17. Territorial attendance patterns during the latter part of the pre-fledging period of great skuas studied in 1987 which left their territories unattended at least once during this period.

pair number	attendance score* 0	1	2	X^2	P**
3	11 (14)	28 (22)	6 (9)	3.28	0.10<P<0.20
7	11 (15)	32 (24)	7 (11)	5.19	0.05<P<0.10
8	5 (12)	41 (27)	7 (14)	18.34	<0.001
9	13 (15)	30 (26)	9 (11)	1.25	0.50<P<0.70
10	1 (5)	20 (12)	6 (10)	10.13	0.001<P<0.01
12	12 (14)	22 (18)	3 (5)	1.98	0.30<P<0.50
13	11 (12)	14 (12)	3 (4)	0.67	0.70<P<0.80
15	6 (8)	24 (16)	2 (6)	7.17	0.02<P<0.05
16	1 (3)	15 (11)	6 (8)	3.28	0.10<P<0.20
19	6 (9)	25 (19)	8 (11)	3.71	0.10<P<0.20
20	1 (7)	28 (16)	2 (8)	18.64	<0.001
22	9 (11)	19 (15)	3 (5)	2.23	0.30<P<0.50
23	8 (12)	28 (20)	6 (10)	6.13	0.02<P<0.05
24	5 (6)	12 (10)	3 (4)	0.82	0.50<P<0.70

continued/

Table 4.17 continued.

	attendance score*				
pair number	0	1	2	X^2	P**
25	8 (11)	29 (23)	8 (11)	3.21	0.20<P<0.30
26	11 (15)	31 (23)	6 (10)	5.45	0.05<P<0.10
27	2 (7)	24 (14)	1 (6)	14.88	<0.001

key:

*. Values given are the number of spot observations of each score made on each pair during the latter part of the pre-fledging period. Values in parentheses are the values expected, given the mean attendance value of each pair, if the skuas were not trying to avoid leaving the territory unattended.
**. Probabilities given are two-tailed.

Table 4.18. Comparison of breeding parameters of Arctic skuas and great skuas studied in the 1970s and in 1987.

1. Arctic skuas

parameter	year 1979*	1987	statistic	P
Internal egg volume (cm^3) **	45.95+/-0.39 (325)	46.62+/-0.88 (52)	d = 1.38	0.10<P
Proportion of pairs laying one egg	35/186 19%	2/28 7%	X^2 = 1.58	0.20<P<0.30
Maximum hatching success (%chicks/eggs)	230/322 71%	46/54 85%	X^2 = 3.81	0.05<P<0.10
Minimum hatching success (%chicks/eggs)	221/322 69%	40/54 74%	X^2 = 0.41	0.50<P<0.70
Hatching success (%chicks/eggs) 1979 max vs 1987 min	230/322 71%	40/54 74%	X^2 = 0.06	0.80<P<0.90
Maximum fledging success (%fledglings/chicks)	214/230 93%	33/40 83%	X^2 = 3.60	0.05<P<0.10
Minimum fledging success (%fledglings/chicks)	205/221 93%	27/46 59%	X^2 = 35.86	<0.001
Fledging success (%fledglings/chicks) 1979 min vs 1987 max	205/221 93%	33/40 83%	X^2 = 3.25	0.05<P<0.10
Maximum post-fledging survival (%juveniles/fledglings)	209/214 98%	6/27 22%	X^2 = 134.05	<0.001
Minimum post-fledging survival (%juveniles/fledglings)	200/205 98%	6/33 18%	X^2 = 147.16	<0.001

continued/

Table 4.18. continued.

parameter	year 1979*	year 1987	statistic	P
Post-fledging survival (%juveniles/fledglings) 1979 min vs 1987 max	200/205 98%	6/27 22%	X_2 = 128.62	<0.001
Breeding success (%juveniles/eggs) 1979 min vs 1987	200/322 62%	6/54 11%	X_2 = 46.52	<0.001
Breeding success (%juveniles/eggs) 1979 max vs 1987	209/322 65%	6/54 11%	X_2 = 52.48	<0.001

2. great skuas

parameter	year mid-1970s***	year 1987	statistic	P
Internal egg volume (cm^3)**	85.91+/-0.21 (749)	83.30+/-0.69 (52)	d = 3.63	<0.001
Proportion of pairs laying one egg	92/881 10%	2/27 7%	X_2 = 0.04	0.80<P<0.90
Hatching success (%chicks/eggs) mid 1970s vs 1987 min	1168/1670 70%	41/52 79%	X_2 = 1.51	0.20<P<0.30
Hatching success (%chicks/eggs) mid 1970s vs 1987 max	1168/1670 70%	44/52 85%	X_2 = 4.53	0.02<P<0.05
Fledging success (%fledglings/chicks) mid 1970s vs 1987 min	1090/1168 93%	16/41 39%	X_2 = 165.30	<0.001

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Table 4.18. continued.

	year			
parameter	mid-1970s***	1987	statistic	P
Fledging success	1090/1168	23/41		
(%fledglings/chicks)	93%	56%	$X_2 = 70.08$	<0.001
mid 1970s vs 1987 max				

key:

*. Data from Furness (1980) except egg volumes which are from unpublished data.
**. Values given are means plus or minus two standard errors. Values in parentheses are the number of eggs measured.
***. Egg volumes from Furness (1977). Other data from Furness (1987a).

Table 4.19. Comparison of the growth rates of skua chicks in the mid to late 1970s* and in 1987.

species	above logistic growth curve**	below logistic growth curve**	X_2	P
Arctic skua (day 0-30)	8 (33.5)	59 (33.5)	38.82	<0.001
great skua (day 0-49)	14 (45.5)	77 (45.5)	23.62	<0.001
great skua (day 0-16)	2 (13)	24 (13)	18.62	<0.001
great skua (day 17-32)	3 (21.5)	40 (21.5)	31.84	<0.001
great skua (day 33-49)	9 (11)	13 (11)	0.73	0.30<P<0.50

key:

*. Logistic growth curve for Arctic skuas from (Furness 1980), and for great skuas, from Furness (1977).
**.Values are the number of 1987 data points which fall above and below the logistic growth curve of skua chicks hatched in the mid to late 1970s. Values in parentheses are the expected distribution of 1987 data points about the logistic growth curve if growth in 1987 was as "good" as in the mid to late 1970s.

Table 4.20. Comparison of 1976 and 1987 census totals for the breeding populations of selected seabird species on Foula. Data from Furness (1987c).

species	unit	1976	1987	% change
kittiwake	AONs	5570	4350	-22
Arctic tern	pairs	5650	300	-95
guillemot	birds	60021	37500	-38
razorbill	birds	10373	6200	-40
puffin	AOBs	70171	48000	-32
gannet	nests	3	124	+4000
great skua hosts	birds to chase	210742	139824	-34
Arctic skua hosts	birds to chase	233176	149000	-36

key:

AONs - apparently occupied nests.
AOBs - apparently occupied burrows.

Table 6.1. Regressions on logmass or mass of various morphological measurements. Gulls (Family Laridae).

measurement	N	b +/- 95% CI	a	r2	P
wingspan*	25	0.27 +/- 0.03	1.34	0.93	<0.001
tail length*	25	0.27 +/- 0.04	0.44	0.90	<0.001
outer tail*	25	0.24 +/- 0.04	0.49	0.88	<0.001
tail area*	25	0.52 +/- 0.07	1.14	0.92	<0.001
planform area*	25	0.58 +/- 0.07	1.62	0.92	<0.001
wing loading*	25	0.45 +/- 0.07	0.27	0.88	<0.001
disc loading*	25	0.49 +/- 0.06	-0.69	0.92	<0.001
humerus*	25	0.35 +/- 0.04	0.04	0.94	<0.001
radius & ulna*	25	0.34 +/- 0.04	0.16	0.93	<0.001
cmc & digit*	25	0.32 +/- 0.04	0.16	0.92	<0.001
cmc*	25	0.31 +/- 0.04	-0.08	0.92	<0.001
major digit*	25	0.33 +/- 0.05	-0.19	0.90	<0.001
lwl**	25	1.0E-5 +/- 7.9E-6	0.20	0.24	0.014
hwli**	25	-3.4E-5 +/- 8.2E-6	0.64	0.76	<0.001
wing camber**	25	-1.0E-5 +/- 9.3E-6	1.09	0.17	0.032
aspect ratio**	25	-3.1E-4 +/- 4.6E-4	9.23	0.08	0.180
fm % of mass**	28	-1.2E-5 +/- 1.1E-5	0.16	0.17	0.032
pmin % of pmaj**	28	6.1E-6 +/- 8.6E-6	0.09	0.08	0.155

continued/

Table 6.1. continued.

measurement	N	b +/- 95% CI	a	r_2	P
smv % of mass**	25	4.3E-6 +/- 5.6E-6	0.06	0.10	0.126
manus % wing**	25	-2.5E-5 +/- 2.6E-5	0.55	0.15	0.057

key:
*. Regressed against log mass.
**. Regressed against mass.
cmc - carpometacarpus
cmc & digit - carpometacarpus and major digit combined
lwl - linearised wing loading,hwli - hand-wing-length index
fm % of mass - percentage of body mass as flight muscles
pmin % of pmaj -pectoralis minor mass as percentage of pectoralis major mass
smv % of mass - standard muscle volume as percentage of body mass
manus % wing - percentage of wing area as the manus

Table 6.2. Regressions on logmass or mass of various morphological measurements. lesser black-backed gulls (Larus fuscus).

measurement	N	b +/- 95% CI	a	r_2	P
wingspan*	10	0.28 +/- 0.13	1.31	0.77	<0.001
tail length*	10	0.32 +/- 0.30	0.28	0.43	0.038
outer tail*	10	0.21 +/- 0.26	0.57	0.31	0.093
tail area*	10	0.59 +/- 0.48	0.94	0.51	0.021
planform area*	10	0.52 +/- 0.42	1.81	0.50	0.023
wing loading*	10	0.48 +/- 0.42	0.18	0.46	0.031
disc loading*	10	0.43 +/- 0.25	-0.53	0.66	0.004
humerus*	10	0.33 +/- 0.19	0.12	0.67	0.004
radius & ulna*	10	0.31 +/- 0.16	0.26	0.71	0.002
cmc & digit*	10	0.34 +/- 0.27	0.12	0.51	0.021
cmc*	10	0.39 +/- 0.26	-0.29	0.60	0.009
major digit*	10	0.31 +/- 0.27	-0.15	0.47	0.030
lwl**	10	1.8E-5 +/- 5.2E-5	0.19	0.07	0.446
hwli**	10	-8.2E-5 +/- 5.0E-5	0.68	0.64	0.006
wing camber**	10	-3.9E-5 +/- 6.8E-5	1.12	0.18	0.219
fm % of mass**	10	2.6E-5 +/- 7.9E-5	0.13	0.07	0.466

key: as for Table 6.1.

Table 6.3. Regression tests of great black-backed gulls (Larus marinus) against lesser black-backed gulls (Larus fuscus).

	wingspan	tail length	outer tail	tail area	planform area	wing loading	disc loading
N(group)	10[a]	10	10	10	10	10	10
r2	0.7680[b]	0.4345	0.3119	0.5067	0.4983	0.4601	0.6591
L marinus	4[c] NS[d] +0.2068[e]	4 NS +0.4582	4 NS +0.5377	4 NS +0.4007	4 NS +0.4426	4 NS +0.4402	4 NS +0.3070

	lwl	wing camber	hwli	humerus	radius & ulna	cmc & digit	cmc
N(group)	10	10	10	10	10	10	10
r2	0.0745	0.1820	0.6376	0.6730	0.7083	0.5079	0.5950
L marinus	4 NS +0.2613	4 NS +0.3169	4 NS +0.1733	4 NS +0.2907	4 NS +0.2628	4 NS +0.4193	4 NS +0.3295

	digit fm	% mass
N(group)	10	10
r2	0.4660	0.0683
L marinus	4 NS +0.4594	4 NS +0.0212*

key:

Abbreviations as in Table 6.1.

a. Number of specimens used for the original group regressions.

b. r^2 for the original group regressions.

c. Number of specimens of the test species.

d. NS indicates that the slope of the new regression line was not significantly different from the slope of the original group regression (** indicates the slope was significantly different).

e. A positive value for r^2 indicates that adding the test species to the regression increased r^2. A negative value (underlined) indicates that adding the test species decreased r^2.

*. see text.

Table 6.4. Regression tests of common gull (Larus canus) against great black-backed gulls (Larus marinus) and lesser-black backed gulls (Larus fuscus).

	wingspan	tail length	outer tail	tail area	planform area	wing loading	disc loading
N(group)	14	14	14	14	14	14	14
r2	0.9748	0.8927	0.8496	0.9074	0.9409	0.9003	0.9661
L canus	1 NS +0.0108	1 NS +0.0246	1 NS +0.0578	1 NS +0.0393	1 NS +0.0256	1 NS +0.0386	1 NS +0.0123

	lwl	wing camber	hwli	humerus	radius & ulna	cmc & digit	cmc
N(group)	14	14	14	14	14	14	14
r2	0.3358	0.4989	0.8109	0.9637	0.9711	0.9272	0.9245
L canus	1 NS +0.0847	1 NS -0.3009*	1 NS +0.0312	1 NS +0.0078	1 NS +0.0047	1 NS +0.0315	1 NS +0.0328

	digit
N(group)	14
r2	0.9254
L canus	1 NS +0.0303

key:
Entries as in Table 6.3.

Table 6.5. Regression tests of herring gull (Larus argentatus) against common gull (Larus canus), lesser black-backed gulls (Larus fuscus) and great black-backed gulls (Larus marinus).

	wingspan	tail length	outer tail	tail area	planform area	wing loading	disc loading
N(group)	15	15	15	15	15	15	15
r2	0.9856	0.9173	0.9074	0.9467	0.9665	0.9389	0.9784
L argentatus	10 NS	10 NS	10 NS	10 NS	10 NS	10 NS	10 NS
	-0.0535	-0.0217	-0.0294	-0.0283	-0.0464	-0.0620	-0.0602

	lwl	wing camber	hwli	humerus	radius & ulna	cmc & digit	cmc
N(group)	15	14	15	15	15	15	15
r2	0.4205	0.4989	0.8421	0.9715	0.9758	0.9587	0.9573
L argentatus	10 NS	12 NS	10 NS	10 NS	10 NS	10 NS	10 NS
	-0.1831	-0.1290	-0.0827	-0.0276	-0.0493	-0.0425	-0.0413

	digit
N(group)	15
r2	0.9557
L argentatus	10 NS
	-0.0555

key:
Entries as in Table 6.3.

Table 6.6. Regression tests of great skuas (Catharacta skua) against all four species of gull studied (Family Laridae).

	wingspan	tail length	outer tail	tail area	planform area	wing loading	disc loading
N(group)	25	25	25	25	25	25	25
r2	0.9321	0.8956	0.8780	0.9184	0.9201	0.8769	0.9182
C skua	18 NS	30 **	32 **	11 NS	18 NS	18 **	18 **
	-0.3423	-0.6740	-0.8601	-0.4316	-0.2514	-0.0697	-0.0922

	lwl	wing camber	hwli	humerus	radius & ulna	cmc & digit	cmc
N(group)	25	26	25	25	25	25	25
r2	0.2374	0.3699	0.7594	0.9439	0.9265	0.9162	0.9160
C skua	18 **	32 NS	18 NS	34 NS	34 **	34 **	9 NS
	+0.1842	-0.3420	-0.0263	-0.1023	-0.4063	-0.2904	-0.2482

	digit
N(group)	25
r2	0.9002
C skua	9 NS
	-0.0021

key:
Entries as in Table 6.3.

Table 6.7. Comparison of morphological parameters which were not significantly correlated with mass between great skuas (Catharacta skua) and the 3 large species of gull studied (Family Laridae).

	gulls		great skuas		
Measurement[a]	n	$\bar{x}$ +/- 2se	n	$\bar{x}$ +/- 2se	P
aspect ratio	24	8.90 +/- 0.15	19	8.61 +/- 0.14	0.005
fm % of mass	27	14.41 +/- 0.36	14	14.80 +/- 0.40	0.090
pmin % of pmaj[b]	17	9.39 +/- 0.34	14	10.52 +/- 0.33	<0.001
pmin % of pmaj[c]	10	8.69 +/- 0.32	14	10.52 +/- 0.33	<0.001
smv % of mass	24	6.57 +/- 0.17	36	6.94 +/- 0.15	0.001
manus % wing	24	50.25 +/- 0.80	19	45.68 +/- 1.22	<0.001

key:
Abbreviations as for Table 6.1.
a. All variables are presented as mean +/- 2 standard errors. All variables, apart from the dimensionless aspect ratio, which are presented in original units (ie percentages) in the table, were trasformed by arcsine transformations prior to carrying out statistical tests.
b. herring gulls (Larus argentatus) and great black-backed gulls (Larus marinus) only.
c. lesser black-backed gulls (Larus fuscus) only.

Table 6.8. Regression tests of Arctic skuas (Stercorarius parasiticus) against all four species of gull studied (Family Laridae).

	wingspan	tail length	outer tail	tail area	planform area	wing loading	disc loading
N(group)	25	25	25	25	25	25	25
r2	0.9321	0.8956	0.8780	0.9184	0.9201	0.8769	0.9182
S parasiticus	3 NS +0.0072	3 ** -0.7113	3 NS +0.0154	3 NS +0.0170	3 NS +0.0045	3 NS -0.1070	3 NS -0.0445

	lwl	wing camber	hwli	humerus	radius & ulna	cmc & digit	cmc
N(group)	25	26	25	25	25	25	25
r2	0.2374	0.3699	0.7594	0.9439	0.9265	0.9162	0.9160
S parasiticus	3 NS -0.2316	3 NS -0.3329	3 NS -0.3002	3 NS +0.0151	3 NS +0.0225	3 NS +0.0199	3 NS +0.0150

	digit
N(group)	25
r2	0.9002
S parasiticus	3 NS +0.0228

key:
Entries as in Table 6.3.

Table 6.9. Comparison of morphological parameters which are not significantly correlated with mass between Arctic skuas (Stercorarius parasiticus) and the 3 large species of gull studied (Family Laridae).

	gulls		Arctic skuas		
Measurement[a]	n	$\bar{x}$ +/- 2se	n	$\bar{x}$ +/- 2se	P
aspect ratio	24	8.90 +/- 0.15	3	9.61 +/- 0.17	0.002
fm % of mass	27	14.41 +/- 0.36	2	19.14 +/- 2.22	<0.001
pmin % of pmaj[b]	17	9.39 +/- 0.34	2	9.55 +/- 1.33	0.390
pmin % of pmaj[c]	10	8.69 +/- 0.32	2	9.55 +/- 1.33	0.044
smv % of mass	24	6.57 +/- 0.17	3	9.81 +/- 0.35	<0.001
manus % wing	24	50.25 +/- 0.80	3	48.31 +/- 1.32	0.035

key:
Abbreviations as for Table 6.1.
a. All variables are presented as mean +/- 2 standard errors. All variables, apart from the dimensionless aspect ratio, which are presented in original units (ie percentages) in the table, were trasformed by arcsine transformations prior to carrying out statistical tests.
b. herring gulls (Larus argentatus) and great black-backed gulls (Larus marinus) only.
c. lesser black-backed gulls (Larus fuscus) only.

Table 6.10. Comparison of morphological parameters between great skuas (Catharacta skua) and Arctic skuas (Stercorarius parasiticus).

	great skuas			Arctic skuas			
Measurement*	n	$\bar{x}$	+/- 2se	n	$\bar{x}$	+/- 2se	P
wingspan[a]	18	1273.5	+/- 14.6	3	1397.4	+/- 49.7	<0.001
tail length[a,c]	30	148.0	+/- 1.8	3	256.0	+/- 21.9	0.005
outer tail[a]	32	134.0	+/- 1.8	3	161.0	+/- 6.9	<0.001
tail area[b]	11	385.9	+/- 12.1	3	525.0	+/- 56.6	<0.001
planform area[b]	18	1893.5	+/- 58.0	3	2033.7	+/- 157.0	0.082
wing loading[a]	18	519.8	+/- 15.6	3	483.8	+/- 35.8	0.094
disc loading[a]	18	77.0	+/- 1.9	3	64.0	+/- 4.6	<0.001
lwl	18	0.230	+/- 0.003	3	0.222	+/- 0.008	0.103
hwli	19	0.590	+/- 0.004	3	0.603	+/- 0.007	0.014
wing camber	34	1.080	+/- 0.004	3	1.068	+/- 0.012	0.108
humerus[a]	34	120.0	+/- 1.4	3	126.0	+/- 5.8	0.029
radius & ulna[a]	34	131.0	+/- 1.4	3	142.0	+/- 5.8	<0.001
cmc + digit[a]	34	122.0	+/- 1.4	3	130.0	+/- 6.9	0.004
cmc[a]	9	65.0	+/- 0.7	3	68.0	+/- 2.3	0.009
digit[a]	9	62.0	+/- 1.3	3	62.0	+/- 4.6	0.811
aspect ratio	19	8.61	+/- 0.14	3	9.61	+/- 0.17	<0.001
fm % of mass	14	14.80	+/- 0.40	2	19.14	+/- 2.22	<0.001
pmin % of pmaj	14	10.52	+/- 0.33	2	9.55	+/- 1.33	0.061

continued/

Table 6.10. continued.

	great skuas			Arctic skuas			
Measurement*	n	$\bar{x}$	+/- 2se	n	$\bar{x}$	+/- 2se	P
smv % of mass	36	6.94	+/- 0.15	3	9.81	+/- 0.35	<0.001
manus % wing	19	45.68	+/- 1.22	3	48.31	+/- 1.32	0.075

key: Abbreviations as for Table 6.1.

*. All variables are presented as mean +/- 2 standard errors.

a. These variables are presented as percentages of $mass^{1/3}$ (units of variables = cm, units of mass = g). For statistical analyses these values were transformed by arcsine transformations.

b. These variables are presented as percentages of $mass^{2/3}$ (units of variables = cm^2, units of mass = g). For statistical analyses these values were transformed by arcsine transformations.

c. A Mann-Whitney U test was used in this case.

Table 7.1 Histochemical characteristics of muscle samples from the pectoralis major, pectoralis minor and iliofibularis muscles of a herring gull and a great skua. Staining intensity is indicated by the number of crosses*.

1.herring gull

muscle block	NADH -TR	α GPDH	mATPase pH of pre-incubation solution 10.5	10.4	10.3	4.65	4.55	4.45	4.35	mean diam**	% popn***
PMj1	3+	3+	5+	4+	-	+	+	+	0	33 +/-0.5	36
	4+	4+	3+	3+	-	+	+	+	0	30 +/-0.4	64
PMj2	3+	3+	4+	4+	-	+	+	+	0	34 +/-0.7	24
	4+	4+	2+	3+	-	+	+	+	0	35 +/-0.7	76
PMj3	3+	3+	4+	4+	-	+	+	+	0	32 +/-0.5	18
	4+	4+	2+	3+	-	+	+	+	0	34 +/-0.5	82
PMn	2+	3+	4+	4+	-	+	+	+	0	51 +/-0.8	33
	3+	2+	3+	3+	-	+	+	+	0	49 +/-1.0	49
	3+	2+	2+	3+	-	+	+	+	0	45 +/-0.9	18
Ilf	3+	2+	5+	4+	-	+	+	+	0	35 +/-1.0	47
	3+	2+	4+	4+	-	+	+	+	0	37 +/-1.0	29
	2+	+	2+	3+	-	5+	5+	4+	3+	47 +/-1.1	24
2. great skua											
PMj1	5+	4+	+	+	4+	4+	2+	0	-	33 +/-0.7	21
	5+	4+	+	+	2+	2+	+	0	-	32 +/-0.7	79
PMj3	5+	4+	+	+	2+	2+	2+	0	-	38 +/-0.8	100
PMn	3+	3+	2+	2+	4+	3+	2+	0	-	48 +/-1.1	30
	4+	4+	+	+	3+	3+	2+	0	-	43 +/-0.9	54
	4+	4+	+	+	2+	3+	+	0	-	42 +/-0.8	16
Ilf	3+	2+	+	+	4+	+	+	0	-	57 +/-1.6	9
	3+	2+	+	+	3+	2+	+	0	-	50 +/-1.3	74
	2+	+	+	+	2+	4+	4+	3+	-	55 +/-1.1	17

key: *. 5+ = very intense staining, 4+ = intense staining, 3+ = moderate staining, 2+ = low staining, + = very low staining, 0 = no staining, - = pre-incubation at this pH not carried out.
**. Values given are mean (micrometres) +/- 2 se.
***. Determined from sections pre-incubated at pH 10·5 (herring gull muscle blocks) or pH 10·3 (great skua muscle blocks).